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SOCIAL LEARNING AND THE DEVELOPMENT OF SOCIAL FORAGING BEHAVIOR IN GOLDEN LION TAMARINS (LEONTOPITHECUS ROSALIA)

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SOCIAL LEARNING AND THE DEVELOPMENT OF SOCIAL FORAGING BEHAVIOR IN GOLDEN LION TAMARINS (*LEONTOPITHECUS ROSALIA*)

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ABSTRACT

Golden lion tamarins are highly social, group-living primates and are cooperative breeders. As such they are an ideal species in which to study social learning. Observations of six groups of wild golden lion tamarins were used to examine the development of social foraging and related behaviors in juveniles. Rates at which juveniles approached adults that were foraging for plant foods tended to decline with age ($F=3.34$, $p=.0531$), and the rates at which they begged ($F=4.71$, $p=.0193$), and foraged at the same site (i.e., co-foraged; $F=3.44$, $p=.0495$) decreased significantly. For prey foraging, rates at which adults vacated a site to allow a juvenile access ($F=7.11$, $p=.0039$), at which juveniles begged ($F=5.41$, $p=.0119$), and co-foraged ($F=5.09$, $p=.0148$) declined significantly with age. Interest in different types of prey foraging substrates and interest in co-foraging also were compared across juvenile age categories. By the time juveniles were in the oldest age category (about one year of age), co-foraging behaviors were still occurring at significantly higher rates than for adults. I investigated two hypotheses concerning the function of co-foraging: the nutrition hypothesis and the information hypothesis. The results most strongly supported the information hypothesis, which predicts that co-foraging provides young tamarins the opportunity to acquire knowledge about food and/or foraging. Behavioral experiments involving vocalization playbacks were carried out with one group of golden lion tamarins at Zoo Atlanta in order to investigate how a specific vocalization, the food-offering call, may influence the development of foraging behavior. The playback experiments contribute to the literature on interactions involving the food-offering call by testing the hypothesis that the call

serves to focus young tamarins on productive foraging sites and thereby facilitates learning about feeding or foraging. Results of this study were inconclusive with respect to whether tamarins are preferentially attracted to foraging sites associated with the food-offering vocalization. However, analysis of tamarin foraging activity during experimentation allowed me to make recommendations for future exploration of tamarin response to the food-offering call.

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CHAPTER ONE

A REVIEW OF SOCIAL LEARNING AND THE ONTOGENY OF FORAGING BEHAVIOR IN CALLITRICHIDAE

SOCIALITY AND SOCIAL LEARNING IN CALLITRICHIDAE

For many animal species, an individual's observations of and interactions with other conspecifics shape much of its behavior. From choosing and obtaining food, to avoiding predators, or choosing a mate, an animal's decisions are often influenced by behaviors it has observed of others since infancy [White & Galef 2000; Galef & Giraldeau 2001; Crane & Ferrari 2013]. Social learning is the term for "instances in which the acquisition of behavior by one animal is influenced by social interactions with others" [Galef 1996]. By learning from others, rather than depending entirely on individual learning, an animal may acquire some knowledge or skill more quickly and with less risk [Galef & Giraldeau 2001]. For example, a young animal with no knowledge of what to eat may choose the same foods as its caretakers and therefore avoid the risk of trying unfamiliar foods that could be toxic [Galef & Giraldeau 2001; Rapaport & Brown 2008]. The alternative to drawing information from observations of others is independent trial-and-error learning. Trial-and-error learning is often not a totally independent process from social learning, however, and a combination of the two strategies may often be necessary for the acquisition of some skill or knowledge. This could be the case in situations where exploration of a location or object by model individuals encourages others to explore the same location/object (enhancement) [van de Waal & Bshary 2011], but further learning about the task is accomplished through trial

and error. Independent exploration may actually be important for preventing the adoption of maladaptive behaviors learned from others [Franz & Matthews 2010]. Nevertheless, social learning is widespread in the animal kingdom, studied in both highly cognitive taxa [Hoppitt & Laland 2008] (birds and primates, with humans being the pinnacle example) as well as some insects [Franks & Richardson 2006; Leadbeater & Chittka 2007]. Research on social learning aids our understanding of the evolutionary processes behind learning strategies and cooperation, as well as the transmission of traditions and culture, in humans and other animals.

Golden lion tamarins are small (average weight is 0.62kg (1.37lbs), diurnal, arboreal primates in the family Callitrichidae [Dietz et al. 1994]. The species is endemic to the Atlantic Forest along the eastern coast of Brazil. Characteristics common to the family Callitrichidae, which includes marmosets, tamarins, and the monotypic *Callimico* genus, make this primate family particularly well-suited for studies of social learning for several reasons.

Callitrichids live in highly social groups, and within these groups they display a high degree of cohesion in both time and space [Digby & Barreto 1993; Fragaszy & Visalberghi 2004]. That is, group members are regularly within close physical proximity to one another, which allows individuals to observe the actions of others [Coussi-Korbel & Fragaszy 1995]. Golden lion tamarin groups are typically comprised of 2 to 11 individuals (mean group size of 5.40) [Dietz et al. 1994], including a single breeding female, one or more breeding or potentially breeding males, and offspring born within the group [Baker et al. 2002]. Lion tamarins, like other callitrichids, are very vocal and use a

number of acoustically distinct calls to communicate and maintain group cohesion [Boinski et al. 1994; Ruiz-Miranda & Kleiman 2002]. Due to the importance of close proximity and peaceful interactions when learning from others, social learning is likely more important for group-living species characterized by highly tolerant and cohesive intragroup relations [Coussi-Korbel & Fragaszy 1995]. For example, callitrichids show a high degree of tolerance to others during foraging and feeding, which may promote social learning. Social foraging activities include: co-feeding/co-foraging (two or more individuals forage in close proximity at the same site) [Rapaport 2006a; Schiel & Huber 2006], scrounging or allowing scrounging [Caldwell & Whiten 2003], food transfers [Moody & Menzel 1976; Izawa 1978; Passos & Keuroghlian 1999; Rapaport & Ruiz-Miranda 2002; Rapaport 2006a], and cooperative problem solving [Werdenich & Huber 2002; Cronin et al. 2005].

Tamarins' high degree of group cohesion and social tolerance is closely related to their breeding system; callitrichids are cooperative breeders, which means that infants and juveniles are regularly cared for by group members other than their parents [Solomon & French 1997; Burkart et al. 2009]. Adult and subadult callitrichid group members help carry offspring that are not their own, provision young with food, and defend them from predators [Garber et al. 1984; Terborgh & Goldizen 1985]. It has been suggested that cooperatively breeding species are more likely to display spontaneous behaviors that benefit others (proactive prosociality) [Burkart & van Schaik 2013], to pay close attention to others, and to engage in social learning, cooperative problem solving, and teaching or teaching-like behavior (relative to taxa with non-cooperative offspring care)

[Rapaport 2006b; Burkart & van Schaik 2010]. The high levels of tolerance shown towards young group members by adults allow opportunities for young to interact with a number of knowledgeable models. Interestingly, callitrichids are the only primates known to be true cooperative breeders other than humans [Hrdy 2001]. This breeding system may have implications for the importance of prolonged caretaking of young for offspring survival in humans and non-human cooperative breeders [Hrdy 2001; Rapaport 2006b; Sear & Mace 2008].

An additional characteristic of callitrichids that may predispose them to high reliance on social learning is their complex diets, which may require a large degree of exploration and learning to fully master [Giraldeau et al. 1994; Laland et al. 1996]. Like other callitrichids, golden lion tamarins are generalist omnivores that feed on a diverse assortment of animal prey and plant parts, all of which vary seasonally [Garber 1993; Martins & Setz 2000; Kierulff et al. 2002]. Plant food items include ripe and unripe fruit, flowers, exudates, and nectar [Kierulff et al. 2002; Procópio de Oliveira et al. 2008]. Prey items include a variety of invertebrates as well as small vertebrates such as lizards, frogs, and fledgling birds [Kierulff et al. 2002; Procópio de Oliveira et al. 2008]. Complex diets pose several challenges, including the necessity of learning how to find and forage for a wide variety of items, and how to avoid harmful and toxic items [Galef & Giraldeau 2001; Rapaport & Brown 2008]. Through social learning, young callitrichids may acquire necessary foraging skills more quickly than if they relied exclusively on independent trial-and-error learning. Social learning from knowledgeable conspecifics may also allow young to advance to foraging independence more safely,

with less risk of handling dangerous prey or ingesting harmful substances [Galef & Giraldeau 2001; Rapaport & Brown 2008].

According to the 'need-to-learn' hypothesis, slower juvenile development is related to complex foraging patterns [Ross & Jones 1999]. Thus, further dietary challenges arise when a significant portion of a species' diet requires complex manipulation or extraction. Unlike other callitrichids, lion tamarins specialize in extractive prey foraging [Dietz et al. 1997]. Their narrow, elongated hands and fingers help them procure much of the protein in their diet by foraging in small knotholes, bromeliads, tree crevices, and other similar substrates [Rylands 1993; Dietz et al. 1997; Bicca-Marques 1999]. This manipulation of foraging substrates is considered a complex foraging strategy because it requires greater sensorimotor coordination and learning than, for instance, gleaning a readily visible insect off the surface of a branch [Gibson 1987; Gunst et al. 2010]. Especially considering the complexity of their habitat, learning which substrates make good foraging sites and how to search each type for prey during extractive foraging may be one of the lengthier processes in the development of lion tamarin foraging behavior. Juvenile lion tamarins' attention to foraging group members may peak several months of age later than that of non-extractive foraging callitrichids because specialization in extractive foraging requires slower development of foraging skills in tamarins [Rapaport 2011]. The comparatively short time it takes the common marmoset (*Callithrix jacchus*), a callitrichid that does not utilize extractive foraging, to reach adult prey-foraging efficiency supports this idea [Schiel et al. 2010; Rapaport 2011]. The results described in Chapter Two of this manuscript support the need-to-learn

hypothesis by providing evidence that co-foraging behaviors peak several months later for golden lion tamarins than in the common marmoset.

SOCIAL LEARNING AND THE ONTOGENY OF SOCIAL FORAGING IN GOLDEN LION TAMARINS AND OTHER CALLITRICHIDS

Young animals face a learning curve for developing the knowledge and skills needed to feed themselves independently. Young individuals are typically less efficient foragers than their adult conspecifics and rely on parental investment in the form of active or passive feeding assistance for a period of time during juvenescence [reviewed in Wright & Leonard 2002; Rapaport & Brown 2008; Sugiyama 2011]. To attain foraging independence, young animals must learn to recognize foraging sites and to obtain and process food for consumption, either through individual learning, social learning, or a combination of the two strategies. For some species, social learning may be crucial for guiding young animals to foraging proficiency more safely and at a younger age than if they had to do so independently [Perry & Ordonez Jimenez 2006].

Many primate species have extended periods of juvenescence during which they are more easily tolerated by adult group members, and therefore have ample opportunity to observe and interact with experienced foragers [Rapaport & Brown 2008]. Adult animals can facilitate learning in young animals in a number of ways. Adult foragers may passively allow learning by permitting young animals to take and eat some of the food that the adult has procured (tolerated theft) [Blurton Jones 1984; Brown et al. 2004]. This behavior, also termed scrounging, is common in callitrichids and other primates [Rapaport & Brown 2008]. Scrounging has been found to inhibit learning of a task in a

number of taxonomically diverse species, because the scrounger focuses on scrounging food, not learning to solve the task [Fragaszy & Visalberghi 1989; Beauchamp & Kacelnik 1991; Lefebvre & Helder 1997]. However, several studies have demonstrated that scrounging can facilitate learning of a foraging task for callitrichids [Caldwell & Whiten 2003; Moscovice & Snowdon 2006] and other cooperative breeders including meerkats (*Suricata suricatta*) [Thorton & Malapert 2009] and Florida scrub-jays (*Aphelocoma coerulescens*) [Midford et al. 2000]. Burkart et al. [2009] and Burkart & van Schaik [2010] suggest that the tolerant nature of cooperatively breeding groups and their propensity for social learning may explain why scrounging facilitates learning in cooperative breeders and not in other species.

Like other callitrichids, golden lion tamarin adults are unusual in that they regularly and willingly provision their young and the offspring of other group members with food items [Garber et al. 1984; Terborgh & Goldizen 1985]. In contrast, weaned juveniles of most non-cooperatively breeding primates do not receive active help when foraging and feeding [Rapaport & Brown 2008]. Adult golden lion tamarins preferentially share foods that are rare, difficult to process, or novel to immatures [Feistner & Chamove 1986; Price & Feistner 1993; Rapaport 1999, 2006a; de A. Moura 2010]. According to the information benefits hypothesis, juveniles may learn which foods to eat based on which foods the adults choose to share during provisioning [Brown & Mack 1978; Feistner & McGrew 1989].

Young callitrichids often forage alongside older group members [Rapaport & Brown 2008]. Foraging alongside conspecifics (termed *co-foraging*) may promote

learning about foraging information and skills for callitrichids and other species. During co-foraging, juveniles have the opportunity to closely observe experienced models [Schiel & Huber 2006]. Foraging and feeding in proximity to conspecifics that are engaged in foraging activities has been investigated in callitrichids [Rapaport & Ruiz-Miranda 2002; Moscovice & Snowdon 2006; Schiel & Huber 2006; Rapaport 2011], and other primates [O'Malley & Fedigan 2005; Jaeggi et al. 2010; van de Waal et al. 2014; reviewed in Rapaport & Brown 2008]. For example, Schiel & Huber [2006] presented evidence that juvenile marmosets seek information from models with whom they forage by paying close attention to models and closely matching models' behavior. Chapter Two of the present work contributes to our knowledge of co-foraging behavior in callitrichids and provides evidence in support of the hypothesis that co-foraging is important for providing informational benefits to young.

Teaching is an advanced form of social learning that is rare among non-human animals compared to other types of social learning. Evidence for teaching exists for a variety of species [reviewed in Hoppitt et al. 2008; Thornton & Raihani 2008], but seems to be particularly common in cooperatively breeding species [Rapaport 2006b; Hoppitt et al. 2008; Burkart & van Schaik 2010]. Examples of teaching or teaching-like behavior in cooperative breeders has been described for golden lion tamarins [Rapaport & Ruiz-Miranda 2002; Rapaport 2006a; Rapaport 2011], common marmosets [Dell'Mour et al. 2009], cottontop tamarins (*Saguinus oedipus*) [Cleveland & Snowdon 1984; Roush & Snowdon 2001; Joyce & Snowdon 2007; Humle & Snowdon 2008], meerkats [Thornton & McAuliffe 2006], tandem-running ants (*Temnothorax albipenni*) [Franks & Richardson

2006], and pied babblers [*Turdoides bicolor*] [Raihani & Ridley 2008]. Wild, adult golden lion tamarins use a particular vocalization, the food-offering call, to alert young group members to the location of living, embedded prey, which the young individual is then allowed to take and process independently [Rapaport 2011]. This adult-directed foraging behavior appears to meet three of the four criteria for teaching behavior according to a functional definition by researchers Caro & Hauser [1992]. The fourth criterion for teaching stipulates that the naïve individual must gain information it may not have learned, or must learn more quickly or efficiently, via interactions with the knowledgeable individual. Chapter Three of this work presents experiments that were intended to help test the fourth criterion of teaching as it applies to adult-directed foraging, by exploring whether tamarins learn a productive foraging site more quickly when the site is associated with the food-offering call.

STUDY SUBJECTS AND AREAS

For the study described in Chapter Two, six groups of wild golden lion tamarins were observed from January 2000 to March 2003 in Brazil's União Biological Reserve (22°27′36″S, 42°02′15″W). The União Reserve is a 3,126 ha area comprised of Brazilian Atlantic coastal rainforest in various successional stages, *Eucalyptus* and scattered feral banana groves, and grassy power line rights-of-way. The Reserve is an IUCN category Ia Strict Nature Reserve under the protection of IBAMA, the Brazilian Environmental Institute, and became Reserva Biológica União (ReBio União) in 1998, affording it a high level of protection according to Brazil's conservation units system [Lapenta et al.

2003; Jenkins et al. 2011]. In addition to the endangered golden lion tamarin, the Reserve is home to a large number of endangered bird species [Jenkins et al. 2011]. Pasture and other deforested lands surround the reserve, leaving it a relatively isolated forest fragment [Jenkins et al. 2011]. In 2008, active reforestation began with the goal of establishing a corridor connecting União with 3,000 ha of neighboring forest [Jenkins et al. 2011].

In 1994-1997 six family groups of wild golden lion tamarins were captured and moved from small, nearby forest islands to the União area [Kierulff & Rylands 2003]. The Reserve's population is descended from these 43 translocated tamarins. Four of the 6 focal groups studied in Chapter Two contained translocated adult tamarins but all of the juveniles and subadults in this study were born within the Reserve.

Golden lion tamarin subjects used for the experiments described in Chapter Three were housed together at Zoo Atlanta in Atlanta, Georgia. The group consisted of 7 individuals, including 3 juveniles. All but one of the subjects was born within the zoo, and the other was transferred to Atlanta in 2009.

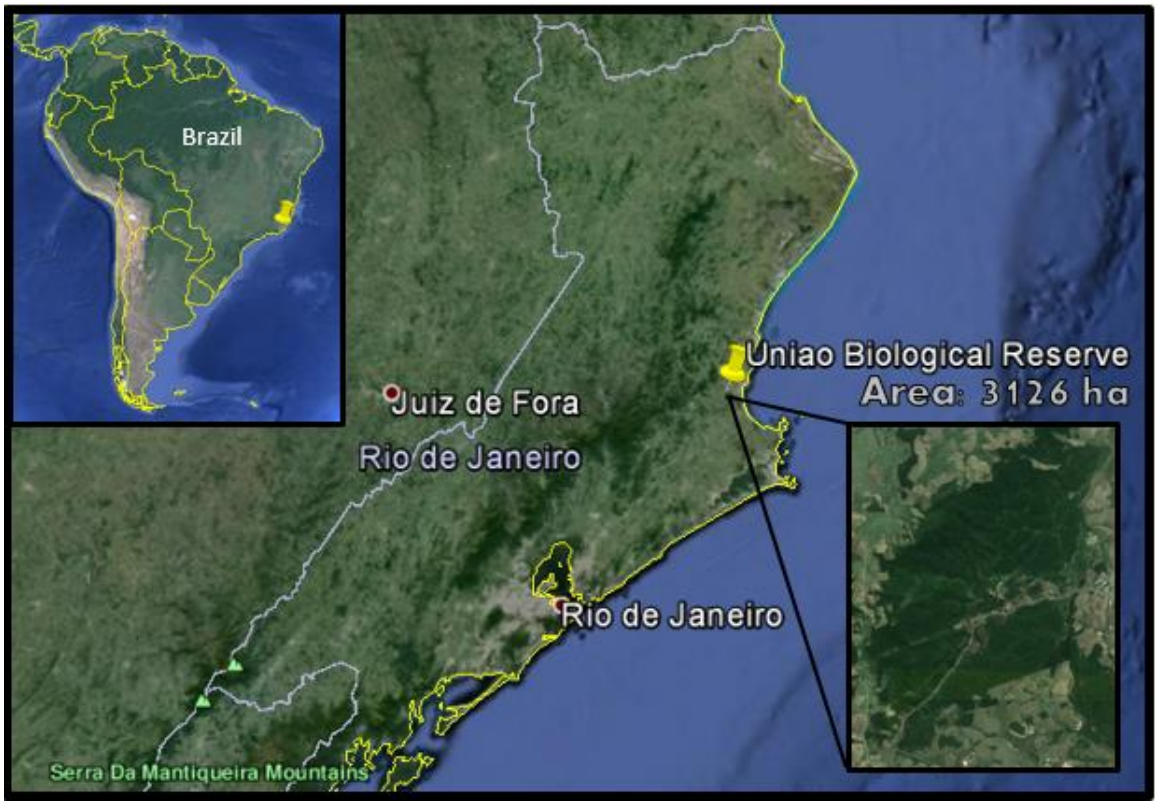

Figure 1.1 The União Biological Reserve is a 3,126 ha protected area of Atlantic coastal forest in the Brazilian state of Rio de Janeiro. It is the second largest track of protected land that provides habitat to the endangered golden lion tamarin (Rylands et al. 2002).

Figure 1.2 Golden lion tamarins at Zoo Atlanta. The above photograph shows several of Zoo Atlanta's golden lion tamarins interacting with the two of the three foraging canisters used in experiments described in Chapter Three of this work.

OBJECTIVES

The overall objective of this study was to examine the development of foraging behaviors, focusing on co-foraging and an experimental examination of the function of food-offering calls in the context of foraging (as opposed to food transfer). Specifically, we asked how co-foraging and food-offering calls may help tamarins learn what, where, and how to forage during juvenile development. This thesis is written in journal style and organized into four chapters. Chapters Two and Three are intended for publication.

The second chapter examines co-foraging behaviors that were analyzed from an observational study, conducted by L. Rapaport and associates listed in the Acknowledgements of this work, of six groups of wild golden lion tamarins at the União Biological Reserve, Brazil. Chapter Two has two objectives: (1) to describe the developmental course of co-foraging behaviors for lion tamarins, and (2) to explore possible nutritional and informational functions of co-foraging. This chapter, titled 'Co-foraging in wild golden lion tamarins', contributes to the body of literature on social learning and social foraging, and to our knowledge of the ontogeny of lion tamarin foraging behavior.

Chapter Three examines lion tamarin response to the food-offering vocalization, which was tested using a series of experiments that I performed on captive zoo golden lion tamarins. The overall objective of Chapter Three was to test a prediction set forth by Caro & Hauser [1992] stating that in order for a behavior (in this case, adult-directed foraging [Rapaport 2011]) to be considered teaching, the naïve individual must gain information it may not have learned, or must learn more quickly or efficiently, via

interactions with the knowledgeable individual. The experiments were designed to answer two questions: (1) does the food-offering vocalization attract tamarins to forage at the site of the call?, and (2) is a foraging site previously associated with the food-offering call preferred in future foraging decisions? This report is titled 'Golden lion tamarin food-offering calls: Response to audio playback vocalizations'. It will be submitted for publication as a brief communication, as it conforms to the content of this type of publication, being based on a single experiment that reports new empirical contributions.

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CHAPTER TWO

CO-FORAGING IN WILD GOLDEN LION TAMARINS

INTRODUCTION

The degree to which social factors influence the acquisition of foraging habits for a species depends on characteristics of their social structure and diet [Cambefort 1981; Milton 1993; Ueno 2005; Rapaport & Brown 2008]. It has been suggested that social learning is particularly adaptive to group-living species characterized by tolerant, non-aggressive social interactions [Coussi-Korbel & Fragaszy 1995], and for species with generalist diets and complex foraging strategies [Giraldeau et al. 1994; Laland et al. 1996; Galef & Giraldeau 2001]. Extensive evidence supports the idea that learning about feeding and foraging from conspecifics can be more efficient and less risky than learning the same information via independent trial and error [Galef & Giraldeau 2001].

Immature individuals are especially likely to depend on social learning when foraging because they are inexperienced at feeding themselves and face a steep learning curve towards foraging independently. Foraging alongside knowledgeable conspecifics (termed *co-foraging*) may facilitate learning about foraging information and skills for young primates [Schiel & Huber 2006; Moscovice & Snowdon 2006; Jaeggi et al. 2010].

Lion tamarins are generalist omnivores, and are known to eat parts of up to 160 different plant species [Kierulff et al. 2002; Procópio de Oliveira et al. 2008], and well as a variety of invertebrates and vertebrate prey [Rosenberger 1992]. They specialize in a type of extractive foraging wherein they use their elongated hands and fingers to search

for hidden prey in a wide variety of vegetative substrates. Substrates that necessitate extractive foraging include crevices and knotholes, bromeliads, dried palm leaf sheaths, broken ends of branch tips, loose and rotting bark, and accumulations of leaf litter and detritus in vine tangles [Rylands 1993; Dietz et al. 1997]. This manipulation of foraging substrates is considered a complex foraging strategy because it requires greater sensorimotor coordination and learning than, for instance, gleaning a readily visible insect off the surface of a branch [Gibson 1987; Gunst et al. 2010]. Especially considering the complexity of their habitat, learning the nuances of extractive foraging (i.e., which substrates make good foraging sites and how to search each type for prey) may be one of the lengthier processes in the development of lion tamarin foraging behavior. The comparatively short time it takes the common marmoset (*Callithrix jacchus*), a callitrichid that does not utilize extractive foraging, to reach adult foraging efficiency supports this idea [Schiel et al. 2010; Rapaport 2011]. According to the 'need-to-learn' hypothesis, slower juvenile development is related to complex foraging patterns [Ross & Jones 1999]. These complex foraging patterns require juveniles to learn proportionally more information or skills in order to become independent foragers. Thus, juvenile lion tamarins' attention to foraging group members may peak several months of age later than that of juvenile marmosets' because specialization in extractive foraging requires slower development of foraging skills in tamarins [Rapaport 2011].

Adult callitrichids show particularly high tolerance towards immatures, often allowing young group members to co-forage and scrounge for food, and actively provisioning young with vegetation and prey foods [Ferrari 1987; Ruiz-Miranda et al.

1999; Rapaport & Ruiz-Miranda 2002; Rapaport 2006]. Adult callitrichids even alter their behavior in ways that promote learning in immatures [Rapaport 1999; Dell'Mour et al. 2009]. For example, adult golden lion tamarins preferentially share foods that are rare, difficult to process, or novel to immatures [Feistner & Chamove 1986; Price & Feistner 1993; Rapaport 1999, 2006; de A. Moura et al. 2010]. Tamarins' high degree of tolerance towards juveniles is closely related to their social system. Like other callitrichids, golden lion tamarins are cooperative breeders – all subadult and adult group members help provision young with food, among other caretaking behaviors [Garber et al. 1984; Terborgh & Goldizen 1985]. Relative to taxa with non-cooperative offspring care, cooperatively breeding species are more likely to display proactive prosociality [Burkart & van Schaik 2013], to pay close attention to others, and to engage in social learning, cooperative problem solving, and teaching or teaching-like behavior [Rapaport 1999, 2006, 2011; Burkart & van Schaik 2010]. Thus, we expect frequent opportunities for social learning about diet to occur in this species, and more opportunities for the transmission of detailed information, relative to those species with less cohesive social groups [Coussi-Korbel & Fragaszy 1995; Fragaszy & Visalberghi 2004]. The age span during which young are highly tolerated by adults is likely an important, highly influential window of opportunity for socially mediated foraging during tamarin development.

Project Aims

Lion tamarins' social structure and diet characteristics suggest that food-related social learning would be adaptive, and previous studies provide strong evidence that callitrichids have the capacity to learn new foods and foraging strategies from others [Bugnyar & Huber 1997; Voelkl & Huber 2000; Schiel & Huber 2006; Voelkl & Huber 2007]. How juveniles become nutritionally independent in the wild, however, is not well understood. Our goal was to explore how social foraging may influence the development of foraging ability and preferences.

The first aim of this study was to describe the developmental time course of co-foraging behaviors in lion tamarins. Since the acquisition of foraging skills may differ for different types of foods, we compare the development of co-foraging behaviors and food acquisition success for plant foods and prey foods separately.

The second aim of the study was to explore possible functions of co-foraging. We considered two hypotheses: the nutrition hypothesis and the information hypothesis. According to the nutrition hypothesis, co-foraging primarily serves to supplement the young tamarins' diets. The information hypothesis predicts that young tamarins acquire knowledge about food and foraging during co-foraging. The two hypotheses are not mutually exclusive but each generates unique predictions.

If the primary function of co-foraging is nutritional then immature tamarins should be most interested in co-foraging for nutritionally dense foods that they have difficulty obtaining by themselves. For the most part, these difficult-to-obtain items are prey foods, which also supply most of the protein and lipid requirements for tamarins

[Erblesdobler 2003; Dietz et al. 1997]. Prey foraging presents more of a challenge to young tamarins than plant food foraging because prey are less visible and less predictable than plant foods. Young tamarins must learn where to find prey and how to handle and process prey for eating. Prey may have defensive mechanisms (e.g., biting or stinging) and may escape without being caught. Plant foods are generally easier for the young to find, obtain and process without help, once the juveniles have accompanied the adults to a fruiting tree. Therefore, if nutritional supplementation is the main benefit to co-foraging, young tamarins should show more interest in co-foraging for prey foods than for plant foods. Next, if nutritional supplementation is an important aspect of co-foraging, we expect that food captured during co-foraging will account for a significant portion of a juvenile's diet. In other words, we would expect rates of food capture success by juveniles during co-foraging to be high, especially for those nutritionally valuable prey.

Alternatively, the primary function of co-foraging may be the transmission of knowledge; that is, co-foraging behaviors may be a mechanism by which young tamarins learn what to eat and where to find food. If the information hypothesis is supported then the youngest juveniles should show high interest in co-foraging for both plant and prey foods. Because many plant and prey foods are still unknown to younger juveniles, co-foraging could provide valuable information benefits for both food types. Since prey foraging presents greater learning challenges, however, young are likely to become proficient vegetation foragers sooner than they become proficient prey foragers. Therefore, we would expect interest in co-foraging for plant foods to decrease more quickly than interest in prey foods as a function of juvenile age. Hidden prey are

hypothesized to be more difficult to obtain than surface prey [Rapaport 2011] and so opportunities to gather the skills needed to learn about hidden prey foraging should be particularly valuable. Thus, young tamarins should be more interested in co-foraging for prey found hidden in substrates (e.g., leaf litter, bromeliads, knotholes) compared to visible prey gleaned from surfaces if they are seeking opportunities to expand their foraging skills. The nutrition hypothesis predicts that interest in hidden and surface prey should not differ; assuming both types of prey are equally nutritious, they are equally valuable targets for co-foraging. Finally, unlike the nutrition hypothesis, support for the information hypothesis does not require high rates of food-capture success during co-foraging, since a co-foraging bout may provide some learning opportunity even if young do not obtain food.

METHODS

Study Site and Subjects

From January 2000 to March 2003, L. Rapaport and associates observed six groups of wild golden lion tamarins in Brazil's União Biological Reserve. The União reserve is a 3126 ha area comprised of Brazilian Atlantic coastal rainforest in various successional stages, *Eucalyptus* and scattered feral banana groves, and grassy power line rights-of-way that traverse the Reserve. In 1994-1997 six family groups of wild golden lion tamarins were captured and moved from small, nearby forest islands to the União area [Kierulff & Rylands 2003]. The Reserve's population is descended from these translocated tamarins.

Four of the 6 focal groups contained translocated adult tamarins but all of the juveniles and subadults in this study were born within the reserve.

We observed 13 juveniles and 34 adults and subadults in the six groups. The juveniles were three successive singleton offspring in one group and a pair of twins in each of the other five groups. In this paper "subadults" refers to individuals 57-112wk of age; the term "adults" will be used to refer to both adults and subadults unless otherwise specified [Hoage 1982; Dietz et al. 1994]. The terms "juveniles", "young" or "immatures" refers to individuals younger than 57 weeks of age. The focal juveniles were studied longitudinally, from approximately 11- 56 weeks of age. By the time formal observations began, all juveniles had been weaned or nearly so. Because food transfer rates peak at about 12 weeks of age in captive lion tamarins, our observations were designed to include the period of maximum provisioning [Tardif et al. 2002]. During biannual captures, the tamarins were marked with hair dye in order to distinguish individuals, and at least one group member was fitted with a radio transmitter collar. Food supplementation (i.e., bananas) by humans was provided only during these trapping attempts.

Data Collection

On a given day, observations focused on either adults and subadults or juveniles. Sessions lasted 20 minutes per individual, and observations on focal individuals were rotated throughout the day in a predetermined order. Data collection usually was carried out from 0630-1430h, with the number of sessions in a single day ranging from 1 to 20.

We employed focal instantaneous sampling with a 120 s interval or continuous sampling, each in conjunction with sequence sampling [Martin & Bateson 1993]. Continuous sampling was used only on two groups and was discontinued 3 months into the study. Observers worked in teams of two, recording data using a palmtop computer for instantaneous or continuous sampling and written notes for sequence sampling. Prior to independent data collection, all observers were trained by L.G. Rapaport for at least two months and interobserver consistency was maintained through regular discussion and simultaneous data collection in the field.

All incidences of the following food-related behaviors involving a focal animal were recorded using sequential sampling: approach, beg, accommodate, and co-forage (see Table 1 for definitions). We recorded instances of food capture during co-forages, identity and size of any food item involved in an interaction, and the substrate on which an individual searched for or obtained food.

Approach	The focal individual moves to within 1 meter of another individual while the approached animal is eating or foraging
Beg	The focal individual closely inspects or reaches for an item that a "partner" has
Accommodate	The initial animal leaves a site from which it has been actively foraging in apparent response to the focal individual's approach within 5 seconds, or the food possessor gives a food call and may hold out food to the approaching focal individual
Co-forage	One individual begins foraging after another individual has already foraged from that same site. One member of the pair must be the focal. If the first individual leaves, the second monkey must forage within 15 seconds of the time the first monkey leaves the site to be considered a co-forage

Table 2.1 Definitions of social foraging behaviors recorded during observations.

Data Sets

Juvenile tamarins were observed for a total of 1330.32 focal-contact hours (a mean of 102.33h + 9.0 per juvenile). We used these data to calculate rates. In addition, we combined 860.22 hours of adult focal-contact data with the juvenile data to calculate proportional measures of interactions involving juveniles (e.g., proportion of approaches by juveniles that resulted in co-foraging with an adult).

The data were collapsed into three juvenile age categories: 11-24 weeks of age, 25-40 weeks and 41-56 weeks. The time that focal individuals spent in visible observation was estimated from the focal instantaneous and continuous sampling methods, which were collected simultaneously with sequence sampling. Thus, rates represent the frequency of a given behavior exhibited by a juvenile or received by that juvenile divided by the estimated time spent in visible observation, for a given period.

Age Block	Age Range (weeks)
1	11-24
2	25-40
3	41-56

Table 2.2 Data were collapsed into three juvenile age categories.

Data Analysis

To examine the timeline of foraging development, we performed linear mixed-model analyses of variance incorporating repeated measures on the rates at which juveniles co-foraged, begged, and approached foraging group members and at which foraging group members accommodated juvenile foraging. Age category was the main effect; we performed this analysis to compare rates of these behaviors across the three juvenile age categories, and rates of behaviors between juvenile age category 3 and adults. We examined co-foraging behaviors for prey and plant foods separately. In order to control for varying rates of approaches and varying rates of co-foraging among individuals, we also used a linear mixed model analysis of variance incorporating repeated measure to examine the following proportions as a function of juvenile age, for both plant and prey foods: (a) the proportion of approaches resulting in co-foraging, (b) the proportion of co-forages where juveniles were successful at obtaining food, and (c) the proportion of approaches where begging occurred.

To analyze juvenile interest in co-foraging for different food types we performed a linear mixed model analysis of variance incorporating repeated measures for (a) rates of approaches to group members foraging on plant substrates versus at prey substrates, (b) the proportion of approaches that resulted in co-foraging by juvenile age blocks for plants versus for prey foraging, and (c) the proportion of approaches that resulted in co-foraging for hidden prey versus for surface prey. Proportion of approaches resulting in co-foraging was used as a measure of interest in co-foraging. We also compared the proportion of co-forages resulting in food capture for plant foods versus prey foods as a

function of juvenile age. Analyses were conducted in SAS. All tests are 2-tailed and with significance level set at $p < 0.05$.

RESULTS

Co-foraging Behaviors by Juvenile Age Blocks

Immature tamarins showed significant differences in co-foraging and begging rates across the three age blocks, for both plant and prey foraging (results summarized in Table 2.3). Rates of approaches and begs to foraging group members, and rates of co-forages, decreased as a function of age, although decreases in approach rates were not significant ($0.1>p>0.05$). When co-foraging (whether for plants or prey) the greatest change in behavior with age occurred between juvenile age blocks 2 and 3.

Rates of plant co-foraging and begging to individuals that were foraging on plant foods decreased significantly with age. Tamarins in the third age block begged to plant foragers significantly less than tamarins in age blocks one or two (Table 2.3). The proportion of plant food co-forages where begging occurred was significantly greater for age block 1 juveniles than for age blocks 2 and 3 (Table 2.5). Tamarins in age blocks 1 and 2 co-foraged for plant foods at similar rates, but a significant decrease in co-foraging rates for plants is seen from age block 2 to 3. Rates of approaches to conspecifics foraging on plant foods showed an increasing trend from age block 1 to age block 2 ($p=0.053$).

Begging to group members that were foraging for prey increased significantly from age block 1 to age block 2, and decreased significantly from age block 2 to 3. For

prey co-forages, the proportion of co-forages where begging occurred did not change significantly across juvenile age blocks (Table 2.5). Thus, begging rates for prey foraging declined more slowly during development than did begging rates for plants. Co-foraging rates for prey in age block 3 were significantly lower than in age block 1 and 2. Adults foraging for prey accommodated juveniles in age block 3 significantly less often than they accommodated juveniles in age block 2. Juvenile approaches to conspecific foraging on a prey item showed a decreasing trend between age blocks 2 and 3.

Behavior: Across Age Categories	Plant * = significant with homogenous variance	Prey * = significant with homogenous variance
Approach	$F_{2,23}$=3.34; p=0.053 Age2 > Age1	$F_{2,23}$=2.84; p=0.0791 Age2 > Age3
Beg	$F_{2,23}$=4.71; p<0.0193 **Age1 & Age2 > Age3** *	$F_{2,23}$=6.07; p<0.0076 **Age1 < Age2 > Age 3**
Accommodate	$F_{2,23}$=2.21; p=0.1319	$F_{2,23}$=7.11; p<0.0039 **Age2 > Age3**
Co-forage	$F_{2,23}$=3.44; p<0.0495 **Age2 > Age3**	$F_{2,23}$=5.09; p<0.0148 **Age1 & Age2 > Age3** *

Table 2.3 Results for the effect of juvenile age on approach, accommodate, beg, and co-forage rates per hour, involving vegetation resources and animal prey. Statistically significant differences are in bold.

Rates of Co-foraging Behaviors: Adults versus the Oldest Juveniles

Even at 10 to 14 month of age, when juveniles were in the third and oldest age category, juveniles approached and co-foraged at significantly higher rates than did adults, for both plant and prey foods (see Table 2.4). Juveniles also were accommodated by adult foragers at significantly greater rates than were other adults.

Interestingly, once we controlled for approach rate (that is, the proportion of co-foraging opportunities that resulted in co-foraging), juveniles in the oldest age category did not differ from adults in the rate at which they co-foraged (Table 2.4). In other words, once the decision to approach a foraging group member had been made, older juveniles were no more likely to co-forage than were adults.

Behavior: Oldest Juveniles (Age 3) vs Adults	Plants	Prey
Approach	$F_{1,33}$=38.57; p<0.0001 **Juv > Ad**	$F_{1,33}$=24.76; p<0.0001 **Juv > Ad**
Accommodate	$F_{1,33}$=9.24; p<0.0046 **Juv > Ad**	$F_{1,33}$=19.25; p<0.0001 **Juv > Ad**
Co-forage	$F_{1,33}$=11.86; p<0.0016 **Juv > Ad**	$F_{1,33}$=14.25; p<0.0006 **Juv > Ad**
Proportion of opportunities (i.e., approaches) resulting in co-foraging	$F_{1,39}$=0.07; p=0.7939 No difference	$F_{1,39}$=1.46; p=0.2348 No difference

Table 2.4 Results for the comparison of juvenile age block three and adult rates per hour of approach, accommodate, and co-forage, and proportion of approaches resulting in co-foraging, involving vegetation resources and animal prey. Statistically significant differences are in bold.

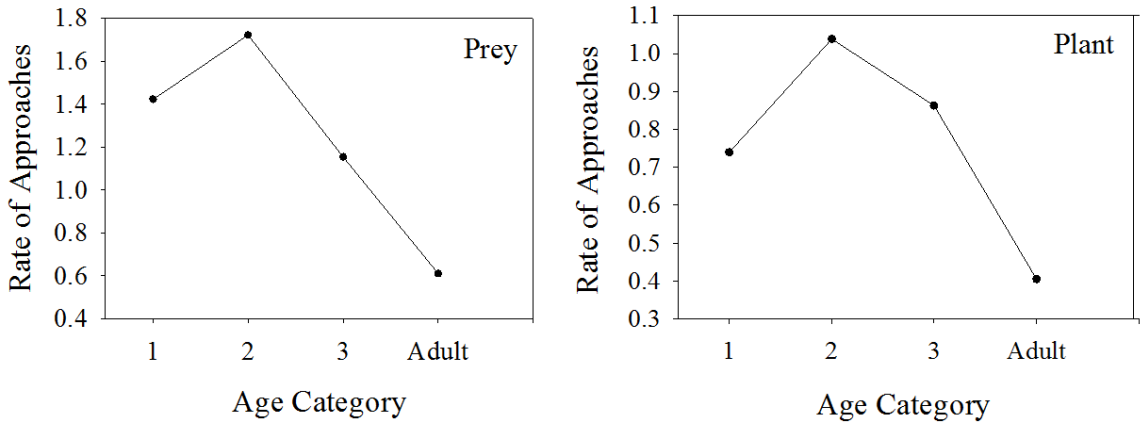

Figure 2.1 Rate of approaches to foraging group members as a function of age for animal prey and vegetation resources. Prey: Age 2 juvenile approach rates were greater than for age 3, but the effect was not significant (p=0.0791), and age 3 juveniles approached at significantly higher rates than did adults (p<0.0001). Plant: Age 2 rates of approach were almost significantly greater than age 1 rates of approach (p=0.053), and age 3 rates were significantly greater than adults rates (p<0.0001).

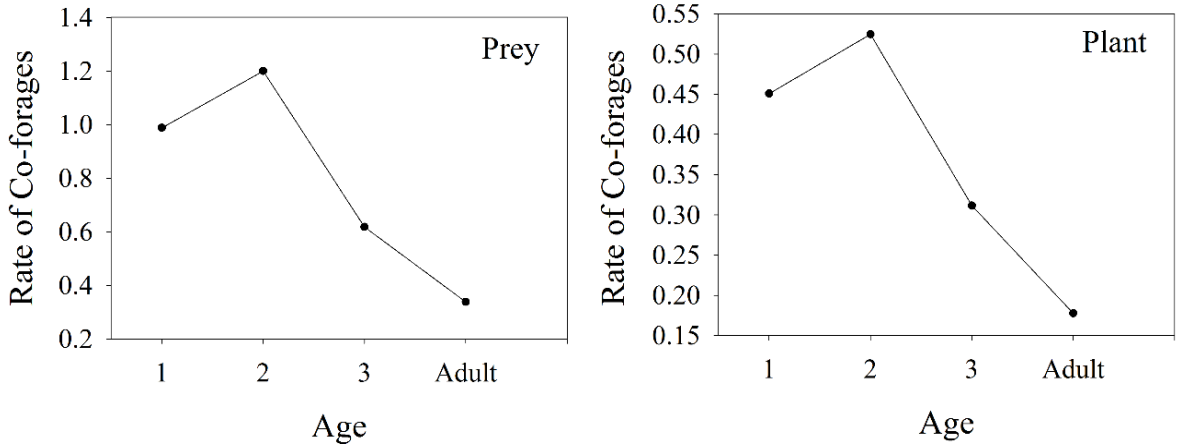

Figure 2.2 Rates of co-foraging as a function of age for animal prey and vegetation resources. Plant: Age 2 rates of co-foraging were significantly higher than age 3 rates (p=0.0495) and age 3 juvenile rates of co-foraging were significantly greater than adult rates (p<0.0001). Prey: Ages 1 and 2 juveniles co-foraged at significantly higher rates than age 3 juveniles (p=0.0148) and age 3 juvenile rates were significantly greater than adult rates (p=0.0006).

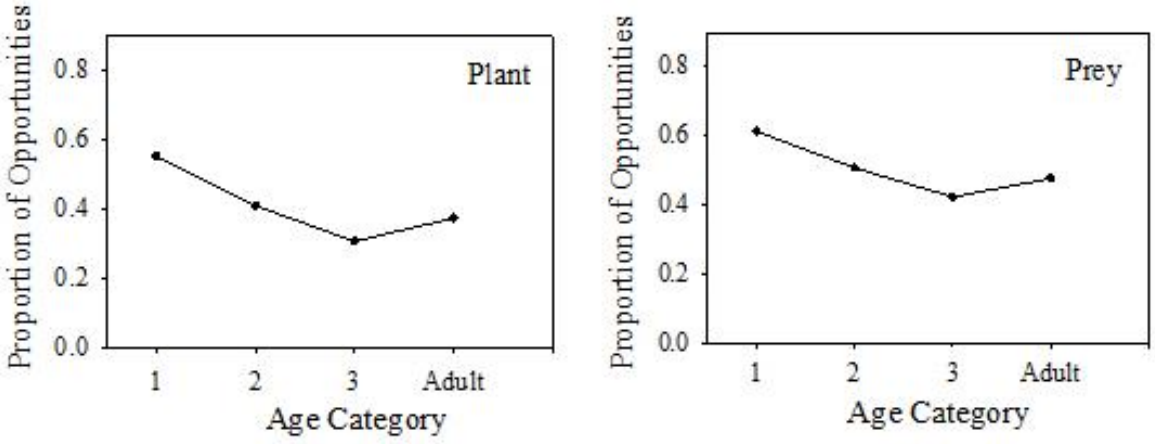

Figure 2.3 Proportion of opportunities (i.e., approaches) resulting in co-foraging as a function of age, for animal prey and vegetation resources. Age 3 juveniles and adults did not differ in their interest in co-foraging given an approach, for either food type (Table 2.4). Prey: Age 1 and age 2 juveniles co-foraged more than age 3 juveniles given an approach, but the effect was not statistically significant (p=0.0578). Plant: Age 1 juveniles did show significantly greater interest in co-foraging relative to age 3 juveniles (p<0.04).

Interest in Co-foraging for Different Food Types

Juvenile rates of approaches to group members foraging on plant substrates did not differ from approach rates to group members foraging on prey substrates ($F_{1,11}$=3.69, p=0.0809). The proportion of opportunities to co-forage (i.e., approaches to a forager) that resulted in co-foraging for plant or prey food is a measure of interest in these two categories of food. Interest in plant foods and prey foods did not differ for juvenile tamarins for any of the age blocks ($F_{1,9}$=1.86, p=0.2053) (Figure 2.4). These results support the information hypothesis. Also, co-foraging given an approach decreases with age for plant food foraging (Table 2.5), and the same pattern was trending for prey foraging, indicating a developmental change.

Juvenile interest in co-foraging for hidden prey items was significantly higher than for surface prey (Table 2.6). This was true for all juvenile age blocks. This also supports the information hypothesis, according to the predictions set forth in the introduction.

Behavior: Across Age Categories	Plant	Prey
Proportion of approaches that resulted in co-foraging (measure of interest in co-foraging)	$F_{2,165}$=3.26; p<0.0410 **Age1 > Age3**	$F_{2,165}$=2.90; p=0.0578 Age1 > Age3
Proportion of co-forages that resulted in food capture	$F_{2,131}$=2.27; p=0.1072 Age1 < Age2 & Age3	Too low to analyze
Proportion of approaches where begging occurred	$F_{2,95}$=6.85; p<0.0017 **Age1 > Age2 & Age3**	$F_{2,95}$=1.13; p=0.3269

Table 2.5 Results for the effect of juvenile age on the proportions of (1) approaches resulting in co-foraging, (2) co-forages resulting in food capture, and (3) approaches where begging occurred, for vegetation resources and for animal prey. Statistically significant differences are in bold.

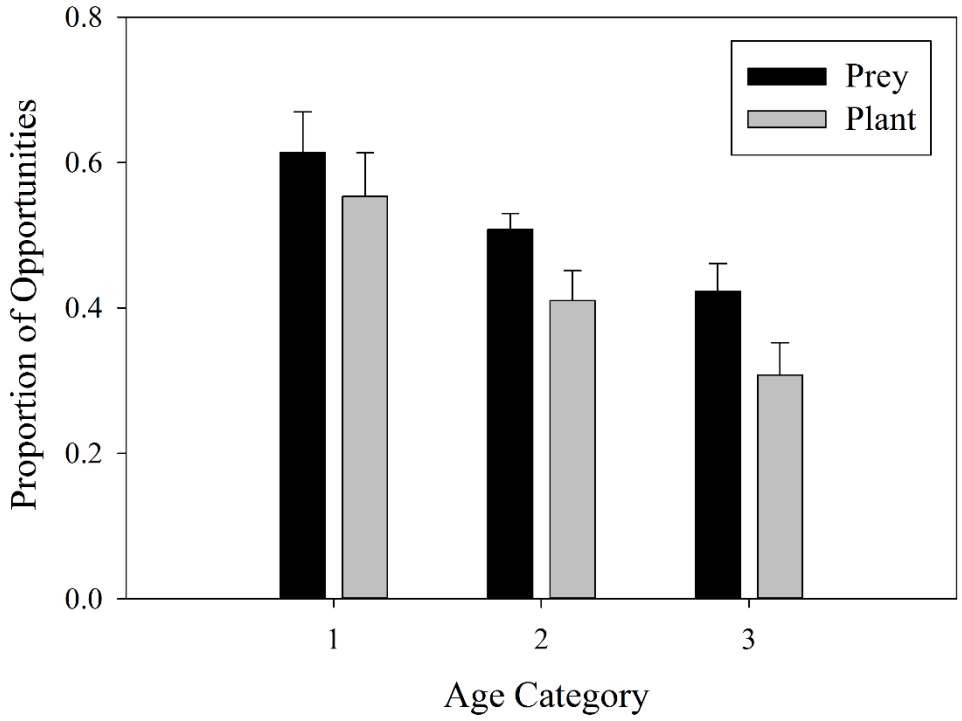

Figure 2.4 Proportion of opportunities (approaches) resulting in co-foraging across juvenile age blocks, for animal prey and vegetation resources. Interest in co-foraging did not differ between plant and prey foods in any of the age categories ($F_{1,9}$=1.86, p=0.2053).

Effect	Juvenile interest in co-foraging for hidden animal prey versus surface animal prey
Age Block	$F_{2,48}$=0.36; p<0.6962 No effect of age on interest in prey type.
Prey Type	$F_{1,48}$=9.21; p<0.0039 **Hidden > Surface**
Age Block x Prey Type	$F_{2,48}$=1.34; p<0.2714

Table 2.6 Results for the effect of juvenile age on interest in co-foraging, for hidden versus surface prey types. Statistically significant differences are in bold.

Co-forage Success

The proportion of an individual's co-forages that result in food capture is a measure of co-foraging success for that individual. At all juvenile age blocks, juveniles were more successful at obtaining plant items while co-foraging than obtaining prey while co-foraging ($F_{1,12}$=125.63, p<0.0001; Figure 2.5). Juveniles were successful at obtaining plant foods during approximately 77-82% of co-foraging bouts. Juveniles were rarely successful at obtaining prey via co-foraging, and only 5.8-8.5% of prey co-foraging bouts resulted in food capture.

The proportion of co-foraging bouts that resulted in obtaining a plant food did not increase significantly as a function of age, although success was slightly lower in the youngest juveniles (Table 2.5). Prey capture success during co-foraging bouts was so low across all ages that statistical analysis was not possible.

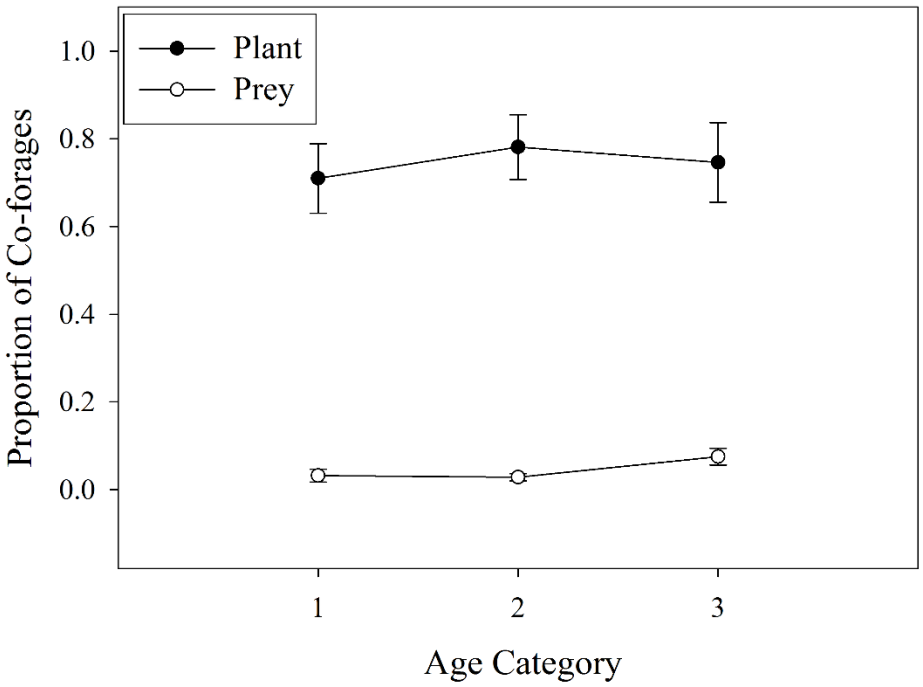

Figure 2.5 Proportion of co-forages that resulted in success (eating) as a function of juvenile age. Success at obtaining vegetation resources was much higher than success obtaining animal prey during co-foraging, for all juvenile age blocks ($F_{1,12}$=125.63, p<0.0001).

DISCUSSION

Timeline of Development

Golden lion tamarin foraging behavior develops slowly. Tamarins in the third and oldest juvenile age block (10-14 months of age) still exhibited foraging behaviors unlike those of adults in that they approached foraging conspecifics and co-foraged more frequently. However, the proportion of approaches that resulted in co-foraging was not significantly different between adults and year-old juveniles. It is unclear why the oldest juveniles continue to approach foragers at higher rates than do adults, but given an approach do not then co-forage at similarly high rates. Since the proportion of approaches resulting in co-foraging decreases during juvenile development, one possibility is that the oldest juveniles, being more proficient foragers, are motivated to co-forage more selectively to fill gaps in their foraging knowledge, rather than to gain immediate access to food. This idea was suggested as an example of how the motivation for food interest behavior might change over the course of juvenile development in white-faced capuchins (*Cebus capucinus*) [Perry & Ordoñez Jiménez 2006].

Juveniles in age block 3 were also accommodated at foraging sites more frequently than were adults. Although an animal's motivation for vacating a foraging site within 5 seconds of another individual's approach cannot definitively be interpreted as a response to the approach, we consider it likely that a significant proportion of accommodate behavior was in response to the focal individual's approach. Therefore, our results suggest that adults are more inclined to relinquish a foraging site to even the

oldest age block of juveniles than to other adults, perhaps reflecting a sensitivity to facilitating foraging efforts of even the oldest juveniles.

Rates of co-foraging behaviors tended to increase from age block 1 to 2 (although this increase was usually non-significant) and then decline in the last age block. Juveniles exhibited the highest rates of co-foraging and begging for plant and prey foods at 6-10 months of age. These rates dropped significantly when 10-14 months old, a point at which juveniles have become more independent foragers [Rapaport 2011]. In comparison, common marmosets, who are not extractive foragers, reach adult foraging proficiency much earlier. For young free-living and captive marmosets, attention to the foraging behavior of group members peaked at around 3-4 months of age [Schiel & Huber 2006; Dell'Mour et al. 2009] and co-foraging behavior began to decrease at 4 months of age [Schiel & Huber 2006]. Common marmoset juveniles have developed adult-like prey foraging abilities by 5 months of age [Schiel et al. 2010]. Thus, our results support the hypothesis that golden lion tamarins' specialization in extractive foraging necessitates a longer period of juvenile development [Rapaport 2011].

Nutrition Hypothesis: Not Supported

At all ages, the proportion of prey co-foraging bouts that resulted in prey capture was extremely low ($\bar{x} = 0.04 \pm 0.008$), which is far too low to provide significant nutritional benefit. If the nutrition hypothesis were the primary driver of co-foraging, we would expect that prey capture success during co-foraging would be higher, considering that 13-15% of an adult lion tamarin's diet consists of prey [Dietz et al. 1997]. The

proportion of plant food co-foraging bouts that resulted in plant food capture was much higher ($\bar{x} = 0.8 \pm 0.033$), so in terms of food capture, juveniles mainly obtain plant foods via co-foraging.

If co-foraging provides little informational value and mainly functions to supplement the diets of young, then young tamarins should be more interested in co-foraging for prey foods than plant foods. This is because juvenile success at capturing prey is very low (less than .25 prey captured per hour until 33-44 weeks of age [Rapaport 2011]), and prey foods are high in nutritional value, so the nutrition hypothesis predicts that juveniles should be more interested in co-foraging for these high-quality foods that they cannot easily obtain themselves. Since juvenile interest in co-foraging did not differ for plants and prey, the nutrition hypothesis was not supported. Considering only animal prey, the nutrition hypothesis predicts that interest in co-foraging would not differ between hidden and surface prey types, but in our study interest in hidden prey was significantly higher than in surface prey.

Lastly, the data show declines in the frequency of co-foraging across age blocks for plant resources. This does not support the nutrition hypothesis because even very young tamarins can forage for most plant foods independently, so the benefit of supplementing the diet with these resources via co-foraging should be very small and are not predicted to decrease over time. Rather, the decrease in frequency of co-foraging for plants could be the result of juveniles accumulating information about new plant foods and thus decreasing their need to learn about plant foods via co-foraging.

Information Hypothesis: Supported

Our study supported the information hypothesis and therefore the idea that co-foraging is important for providing information about food- or foraging-related activities to young lion tamarins. Specifically, young juveniles' interest in co-foraging for plant food items and prey food items did not differ, but interest in co-foraging for hidden prey was greater than for surface prey. Many plant and prey foods are unknown to the youngest immatures, so it follows that they should be highly interested in co-foraging for both types of food in the youngest age block if co-foraging is important for learning. Juvenile interest in co-foraging decreased across age blocks, reflecting increased foraging independence for older juveniles. Although juveniles continued to show no statistically significant preference for co-foraging for either prey or plant foods across all age blocks (approach rates and interest in the two food types stayed the same), interest in plant food co-foraging decreased more quickly than interest in animal prey co-foraging. This makes sense if prey foraging presents greater challenges than plant foraging, because we would expect a longer learning trajectory for prey foraging skills. Similarly, begging rates for prey foraging declined more slowly during development than did begging rates for plants, which also may reflect quicker plant foraging skill acquisition during development.

In our study, juvenile interest in co-foraging for hidden prey was higher than for surface prey. These results are in agreement with other evidence that social foraging tends to involve foods (often prey) that juveniles find difficult to acquire or process on their own [reviewed in Rapaport & Brown 2008]. For example, immature white-faced capuchins (*Cebus capucinus*) were found to pay more attention to group members'

feeding and foraging activities for foods that were difficult-to-process, such as animal prey and fruit with stinging hairs [O'Malley & Fedigan 2005; Perry & Ordoñez Jiménez 2006]. Similarly, when transferring foods to juveniles, adult golden lion tamarins were more likely to actively initiate transfers of difficult-to-handle prey (e.g., prey with defense mechanisms or live prey which could escape) than more easily processed prey [Rapaport 2006]. Our results indicate that young tamarins seek out opportunities to co-forage for hidden prey (i.e., prey requiring extractive foraging), which poses a greater challenge than surface prey. Thus, co-foraging may be particularly important for helping young tamarins become independent *extractive* foragers.

If the Informational Hypothesis is Supported, What Are They Learning?

Young lion tamarins have a lot to learn in the process of becoming independent foragers given their diverse diet and complex environment. They must learn which foods are safe, how to process foods for eating, and where to find food. To know exactly what knowledge young lion tamarins are gaining via co-foraging would require rigorous experimentation and is beyond the scope of this study. Since juveniles' interest in co-foraging for hidden prey was higher than for surface prey, perhaps the ability to identify good prey foraging substrates is learned, at least in part, via co-foraging. Evidence that social learning may be important for helping young animals learn to identify good prey foraging microsites exists for meerkats (*Suricata suricatta*) [Thornton & Hodge 2009], blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) [Slagsvold & Wiebe 2007]. Alternatively, co-foraging simply may reduce neophobia to all foraging sites and

individuals learn which sites are good for finding prey via trial and error. However if this were true, juveniles would not need to observe model foragers at close range [Perry & Ordoñez Jiménez 2006], which they do during co-foraging.

Proximity to feeding and foraging model conspecifics has been investigated in brown capuchins (*Cebus apella*) [Fragaszy & Visalberghi 1990, Boinski et al. 2003], Japanese macaques (*Macaca fuscata*) [Ueno 2005], vervets (*Cercopithecus aethiops)* [Hauser 1988], yellow baboons (*Papio hamadryas cynocephalus*) [King 1994], mantled howler monkeys (*Alouatta palliate*) [Whitehead 1986], big brown bats (*Eptesicus fuscus*) [Wright et al. 2011], rooks (*Corvus frugilegus*) [Dally 2008], bumblebees (*Bombus* spp.) [Leadbeater & Chittka 2007, 2009], common marmosets (*Callithrix jacchus*) [Schiel & Huber 2006], cottontop tamarins (*Saguinus oedipus*) [Moscovice & Snowdon 2006; Humle & Snowdon 2008], meerkats (*Suricata suricatta*) [Thornton & Malapert 2009], and others. Though only some of these studies focused on social learning during juvenile development, all found evidence that social learning mechanisms influence foraging preferences. For example, infant and juvenile marmosets who co-foraged with an adult conspecific were less neophobic towards novel foraging tasks and were attracted to a model individual's foraging site and to the food item the model was examining, which suggests learning via local and stimulus enhancement [Schiel & Huber 2006]. Other laboratory studies have provided evidence that callitrichids learn about novel foods via social facilitation and may even have the potential to imitate the behavior of conspecifics [Bugnyar & Huber 1997; Voelkl & Huber 2000; Voelkl & Huber 2007]. Socially mediated foraging behavior, including co-foraging, in wild callitrichids might also

involve enhancement and imitation learning. Further exploration of what the young tamarins are attending to during co-foraging may help us better understand the functions of co-foraging. For example, if juveniles attend to specific foraging substrates, this could indicate local enhancement; attending to specific food items could indicating stimulus enhancement [Schiel & Huber 2006].

Informational and Nutritional Benefits are Both Likely

Clearly informational and nutritional payoffs from co-foraging are not mutually exclusive and probably are both valid. If immature tamarins are acquiring any food via co-foraging, which they do, then the behavior contributes to their diet to some extent. In summary, our results support the information hypothesis by providing evidence that co-foraging helps juvenile lion tamarins learn how to forage independently for both plant and prey foods, and especially for prey that require extractive foraging.

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CHAPTER THREE

GOLDEN LION TAMARIN FOOD OFFERING CALLS: RESPONSE TO AUDIO PLAYBACK VOCALIZATIONS

INTRODUCTION

Cooperatively breeding species including primates in the family Callitrichidae (marmosets and tamarins) are unusual because of the extent to which adults help care for young group members, even those other than their own offspring [Solomon & French 1997; Burkart et al. 2009]. For young callitrichids, a critical component of parental and alloparental care is the regular provisioning of food after weaning [Garber 1984; Terborgh & Goldizen 1985]. Adults of some callitrichid species, including the golden lion tamarin, emit a specialized food-transfer vocalization to initiate provisioning by signaling to young group members to come take food from the caller [Feistner & Price 1991; Ruiz-Miranda et al. 1999; Roush & Snowdon 2001; Joyce & Snowdon 2007]. Rapaport [2006] reported 79 instances of wild golden lion tamarin adults offering prey items that were preceded by food-offering vocalizations. The vocalizing adult was approached only by juveniles, with one exception in which another adult approached the vocalizing individual, who in this case did not give up the food item. Adults were only observed emitting food-offering calls prior to transfers of prey items, and adults were twice as likely to call before transferring live prey items, which are exceptionally difficult for immatures to capture and handle alone [Rapaport 2006]. Juveniles between 21-32 weeks of age were the most frequent recipients of food transfers initiated by the food-offering call [Rapaport 2011].

Beyond initiating the transfer of in-hand food, adult golden lion tamarins use the food-offering vocalization in a different context when communicating to older juveniles in the group [Rapaport 2011]. Rapaport and Ruiz-Miranda [2002] and Rapaport [2011] describe, in total, 15 instances in which adult golden lion tamarins appear to use the food-offering call to alert young group members to the location of living, embedded prey, which the young individual then extracted and processed independently. For example, an adult foraging in a tree knothole would emit the food-offering call, which encouraged a young group member to approach, forage in the knothole, and independently capture a prey item. This behavior, termed "adult-directed foraging," was almost exclusively reserved for juveniles older than 20 weeks of age [Rapaport 2011].

Adult-directed foraging may be an example of teaching, in which young are presented with a situation that facilitates learning about which types of foraging substrates are good for finding prey [Rapaport 2011]. The behavior appears to meet at least three of the four criteria to be considered teaching, according to Caro & Hauser's [1992] definition. Adults only perform adult-directed foraging behaviors in the presence of naïve individuals, which satisfies Caro & Hauser's first criterion, and adult-direct foraging provides juveniles with age-appropriate experience, satisfying Caro & Hauser's third criterion [Rapaport 2011]. The second criterion for recognizing teaching behavior states that the knowledgeable individuals involved in teaching must incur a cost, or at least gain no immediate benefit, from the interaction; adults were not shown to gain an immediate benefit from adult-directed foraging. The fourth stipulation for teaching is that the naïve individual must gain information it may not have learned, or must learn

more quickly or efficiently, via interactions with the knowledgeable individual [Caro & Hauser 1992]. The Rapaport [2011] study could not determine whether young tamarins actually learn about foraging substrates from adult-directed foraging.

During food transfer and adult-directed foraging, juveniles may learn how to capture and process prey for eating. In this study, we are interested in whether food transfers and adult-directed foraging help juveniles learn where to find prey foods. We ask if interactions involving the food-offering vocalization help juveniles learn either how to recognize productive foraging substrates or how to recognize specific locations in the habitat that are good for prey foraging. The functions of the food-offering vocalization are difficult to assess in the wild due to the challenge of controlling for the position and type of foraging sites across multiple trials. An experimental approach, on the other hand, offers the type of controlled foraging situation necessary to tease apart these alternative possibilities. In the present study, audio playback recordings of the food-offering vocalization were used to assess whether food-offering calls help tamarins learn which foraging substrates are productive, which would support the idea that adult-directed foraging satisfies Caro & Hauser's fourth criterion for teaching. We sought to test two hypotheses regarding the role of food-offering vocalizations during foraging ontogeny: (1) the food-offering vocalization encourages foraging at substrate types or substrate locations from which the vocalization recording is emitted, and (2) the food-offering vocalization influences future foraging behavior by resulting in increased foraging at substrates or foraging locations previously associated with the vocalization.

We used a set of three foraging canisters painted with different designs that were meant to represent different foraging substrates. If the food-offering call influenced future foraging behavior, then we would further test whether tamarins associated the vocalization with the properties of the foraging substrate (i.e., canister design) or with the position within the enclosure. This would provide insight into what type of information juveniles may attend to during adult-directed foraging. If tamarins learned to focus their foraging efforts at the canister from which the food-offering call was previously emitted, this would provide evidence that the food-offering call serves to focus juvenile's attention on particular characteristics of foraging substrates. That is, they may learn which types of substrates are good for finding prey foods via during adult-directed foraging. Alternatively, if tamarins learn to focus foraging activities on the positions in the enclosure from which the food-offering call was previously emitted, this would suggest that the tamarins perceive the food-offering call as indicative of a productive foraging location. If this is the case, then during interactions involving the food-offering call, juveniles may learn specific locations (e.g., specific feeding trees) where prey foraging is good.

We tested the tamarin group under two conditions. In the first condition (condition one), tamarins were allowed to interact with the set of three foraging canisters while either canister 3 (C3) or canister 2 (C2) contained a food reward. When C3 contained the food reward, the food-offering call playback was emitted from C3. The playback was never emitted from either C2 or canister 1 (C1). C1 never contained a food reward. In the second condition (condition two), the tamarins were allowed to interact

with the same set of foraging canisters, but none of the canisters contained a food reward or emitted the food-offering playback. In other words, in condition one, the tamarins had the opportunity to find a hidden food reward in one of two possible, randomly placed canisters. The third canister did not contain food. In condition two, the canisters were presented in different locations and none contained food.

Condition one tested the prediction that the food-offering vocalization immediately attracts tamarins to forage at the site of the call. Based on accounts that juveniles readily search for embedded prey after being directed to a foraging site by a food-offering vocalization [Rapaport 2011], we predicted that tamarins would show increased exploration of foraging substrates associated with food-offering calls. We expected this effect to be particularly strong for tamarins younger than 44 weeks of age (n=3), which is the age at which most adult-directed foraging took place in the wild [Rapaport 2011].

Condition two allowed us to test whether the food-offering call serves to attract the tamarins to either the canister design or the canister position. That is, does the call facilitate learning about the location of prey-foraging sites or about the type of substrate on which prey may be found? If the food-offering call playback did influence tamarins to prefer certain foraging positions or a certain canister design, we would expect tamarins to increasingly concentrate their foraging efforts at either (1) the canister design from which the call was emitted in the previous trial, or (2) the canister position from which the call was emitted in the previous trial. If this prediction were supported, it would provide evidence that young tamarins do learn how to recognize productive foraging sites via

adult-directed foraging, thus supporting the idea that adult-directed foraging satisfies the fourth and final criterion of Caro & Hauser's definition of teaching.

METHODS

Subjects and Housing

Seven golden lion tamarins from a captive family group at Zoo Atlanta participated in this study. The group consisted of one juvenile born in June 2013, two juvenile twins born March 2013, and four adults (see Table 3.1). The group shares one climate-controlled habitat that includes an off-exhibit space containing the nest box, and a glass-front exhibit. The exhibit was furnished with tree branches and a few small enrichment items. The group was fed twice a day: once between 0830-1000 hours and again between 1300-1500 hours, and water was available ad libitum.

Name	DOB	Born at Zoo Atlanta?
Robin	06/2006	Y
Theo	03/2006	N (Transferred Aug 2009)
Eva	07/2012	Y
Tiete	04/2011	Y
Leao	03/13	Y
Pele	03/13	Y
Unnamed	07/13	Y

Table 3.1 Golden lion tamarin study subjects housed at Zoo Atlanta in Atlanta, Georgia, USA.

Foraging Apparatuses

The foraging apparatuses were three cylindrical sections of bamboo, 33.02cm long x 5.08cm in diameter, each with two holes approximately 5.08cm x 2.54cm. The foraging actions required by the substrates involved peering into and inserting an arm into the holes of a container to search through cardboard shavings for food rewards. To prevent tamarin injury, the edges of all openings in the canisters were sanded to create smooth edges. The apparatuses were designed to simulate the visual and tactile foraging actions involved in extracting embedded prey. A smaller section of bamboo was attached beneath each foraging apparatus using zip ties; the voice recorder having the food-transfer call recording was contained here for C3 in some trials. We used an Olympus Voice Recorder WS-700M with a recording of a food-transfer vocalization obtained by us in April 2013 from the Zoo Atlanta golden lion tamarin group. The vocalization lasted 4 seconds and was recorded onto the device so that it was repeated 5 times per each trial where it was used: once at 1min into the recording and then again every 30s until 3min into the recording. Repetition ensured that all group members heard the playback call and increased the likelihood that all group members discerned the general position and/or canister from which the playback call was emitted. Based on previous experiments involving food playback calls and common marmosets [Kitzmann & Caine 2009], we would not expect to see a change in foraging behavior simply in response to the sound of a playback call unless it was related to feeding or foraging.

The three food canisters we used were differentiated from one another by pattern, with each pattern representing a different type of foraging substrate (See Figure 3.1A).

The apparatuses were suspended just under tree limbs that were already inside the tamarin enclosure and were spaced as far apart as the enclosure allowed, so that a food-offering playback call was easily associated with only one of the containers. Figure 3.1B shows the relative positions of the canisters inside the enclosure. Grapes were used as a food reward, except for in the first trial on October 06, 2013 where mealworms were used. Both grapes and mealworms are highly preferred foods [Benz 1993]. Between trials, the cardboard chips inside the foraging canisters were replaced and the canisters were cleaned with alcohol swabs to reduce any odors (e.g., from the grapes or scent marking).

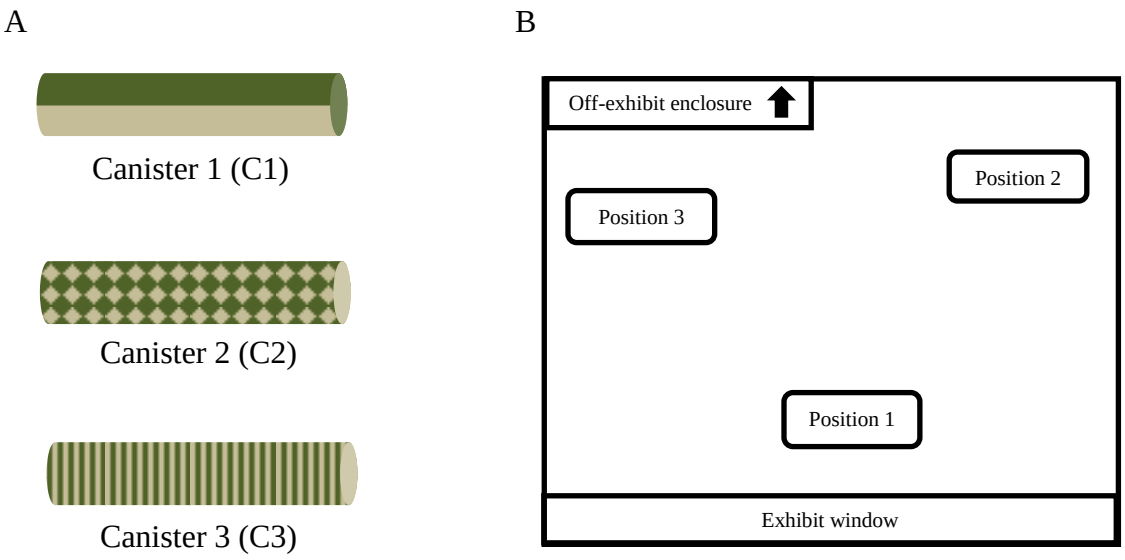

Figure 3.1 A) Foraging canister designs. Two colors of paint, one light and one dark, were used to create one apparatus with wide stripes, one with large spots, and one split in half by color. B) Layout of tamarin enclosure. The canisters were moved between three positions in the enclosure, spaced as far apart as possible to create discrete foraging sites.

Experimental Design and Procedure

Experimental sessions took place twice a day on 9 days between October and December 2013. Trials 1 and 2 took place on October 27; Trials 3-10 took place from Dec 06-09, and trials 11-18 took place from December 13-16. In order to ensure that tamarins would be highly motivated to explore the foraging canisters, trials took place before normally scheduled feeding times: once between 0830 and 0930 hours and again between 1330 and 1430 hours. All tamarins in the enclosure were coaxed from their nest box room into the exhibit section of their habitat before the foraging canisters were hung in place. All experiments were videotaped. Data collection began once all canisters were in place and the keeper left the enclosure and ended 10 minutes thereafter.

Condition One: Do food-offering calls emitted from a specific foraging substrate make that foraging site more attractive?

Each of the three canisters was associated with a different foraging condition: C3 contained food and emitted the food-transfer vocalization, C2 contained food and did not emit the vocalization, and C1 served as a control and never contained food and did not emit the vocalization. For trials of condition one, C3 and C2 alternated between having food and not having food for each trial. So, for example, on a trial when C3 had the food reward (every other trial of condition one), the food-offering vocalization recording was played on the recorder in the compartment attached to canister 3, and no other canister was baited. In the next trial, none of the canisters had food (condition two). On the trial after that, C2 would contain food (but no food-offering call) and no other canister was baited.

The positions of the containers were changed relative to the previous trial so that none of the canister designs, nor the baited or un-baited condition, were associated with any one location in the enclosure. This allowed us to test whether the food-offering call was attracting the tamarins to canister type or position without confusing the effect of a preexisting preference for foraging at certain locations or the effect of having the food-reward always appear at the same locations. Rather than selecting canister positions at random, we attempted to assign canister position so that over the course of the experiment, each canister had been located in a given position (e.g., canister 3 at position 1) relative to the other canisters and their positions (e.g, when canister 2 was in position 1 and canister 1 was in position 3) an approximately equal number of times.

For trials of condition one, we hypothesized that the tamarins would show an *overall* stronger preference for foraging at C3 (food reward + food offering call) over C2 (food reward, no food-offering call), even if they preferred to forage at canister 2 during trials where canister 2 had the food reward. We expected that the tamarins would prefer to forage at C2 and C3 over C1 for all trials, but especially in later trials if they learn to associate canisters 2 and 3 with the food reward.

Condition Two: Is the substrate type or foraging site previously associated with a food-offering call more attractive than other substrate alternatives in the future?

For condition two we presented the same foraging canisters as in condition one, but in the absence of any food rewards or audio playback cues. That is, the canisters only contained cardboard chips and the food-offering vocalization did not play. Trials for condition two were alternated with trials for condition one so that conditions more

closely mimic the experience of wild tamarins and to reduce the possible effect of training the tamarins to respond to food-offering calls. The three foraging canisters were attached to the enclosure, spaced in a different arrangement for each trial, as in condition one (Table 2).

Condition	Trial	Canister at Position 1	Canister at Position 2	Canister at Position 3
1	1	3⌂	2	1
2	2	2	1	3
1	3	1	3	2
2	4	2	1	3
1	5	2	1	3⌂
2	6	3	1	2
1	7	3	2	1
2	8	2	1	3
1	9	3⌂	1	2
2	10	1	2	3
1	11	2	3	1
2	12	3	1	2
1	13	2	1	3⌂
2	14	1	3	2
1	15	3	2	1
2	16	2	3	1
1	17	3⌂	1	2
2	18	1	2	3
⌂ = playback call highlight = food reward				

Table 3.2 Summary of experiment design. Trials of condition one correspond to odd-numbered trials. Trials of condition two correspond to even-numbered trials. Highlighted cells indicate the canister that contained a food-reward. The ⌂ symbol indicates when C3 emitted the food-offering vocalization.

Data and Analysis

Durations and counts of foraging bouts were collected from video recordings to ensure accuracy. Individual tamarins were identified by their natural physical differences. For our purposes, individuals Eva and Teite were indistinguishable from one another and individuals Laeo and Pele were indistinguishable from one another, but both pairs were distinguishable from all other individuals. For data collection and analysis, pair Eva-Teite and pair Laeo-Pele were each treated as a single individual. Individuals Robin, Theo, and the unnamed youngest tamarin were readily distinguishable from other individuals. For 98.86% of foraging bouts, the foraging individual was identified to this extent (1387 of 1403 total foraging bouts). Foraging bouts where the individual was not identifiable were excluded from analyses. Adults and juveniles were analyzed separately in order to assess age-related differences in reaction to the food-offering call. We also analyzed responses to the foraging canisters during the entire 10 minutes of trials and during only the first three minutes of the trials. Our purpose for limiting analyses to the first 3 minutes was to get a clearer idea of where the tamarins were most interested in foraging, by limiting our analysis to foraging decisions at the start of the trials.

For each individual, we measured the duration of each foraging bout at each canister for every trial. The total duration of all foraging bouts at each canister was summed to obtain a total time spent foraging at each canister per trial for each individual. We also measured the number of foraging bouts for each individual at each canister per trial. We performed a linear mixed model analysis of variance incorporating repeated measures for time spent foraging at each canister and number of visits to each canister.

Each of these dependent variables was considered for both the full 10-minute trial duration and for only the first 3 minutes of trials. All analyses were conducted in SAS. Analyses focused on four questions:

(1) Was food the primary motivator for tamarins deciding where to forage?

This test was important for discovering if the tamarins were strongly attracted to the canister that contained a food reward.

(2) Did the food-calls act as an attractant for foraging activities?

If food-offering calls attract tamarins to a foraging site, then across the baited trials, we would predict significantly more foraging effort at C3 (which had the playback vocalization) when C3 was baited than at C2 when C2 was baited.

(3) Did the food-offering vocalization playback influence the tamarins to concentrate their foraging efforts on (a) the position within their enclosure where the food-offering call was emitted? Or (b) the specific canister design (C3) from which the food-offering call was emitted?

If tamarins learn to perceive the food-offering call as indicative of a productive foraging position within the enclosure, we would predict that during the non-baited trials they would forage preferentially at the position from which the playback had been emitted in the previous trial. If tamarins learn to perceive the food-offering call as indicative of a productive canister design, we would predict that during non-baited trials, they would be significantly more interested in foraging at C3, especially during trials immediately following trials in which C3 had had food and had emitted the playback. This prediction assumed that the

tamarins would prioritize the most recent information (i.e., memory of which canister/position contained food and/or emitted the food call in the previous trial) in their foraging decisions.

(4) How did tamarin foraging preferences change over the course of the trials?

If tamarins learn to perceive the food-offering call as indicative of a productive canister type, they should show an increasing preference for foraging at C3 over the course of the experiment. They should also show an increasing preference for foraging at C2 since C2 sometimes contained the food rewards, but we expected this effect to be less pronounced than for C3. We would expect a decreasing preference for foraging at C1 over time because this canister never contained a food reward.

RESULTS

Food Motivation

Adults were more motivated than juveniles to forage at the canister that contained a food reward for our study. To test whether the tamarins were primarily motivated by the presence of a food reward in their foraging decisions, we considered the baited trials only. We performed a linear mixed model analysis of variance incorporating repeated measures on time spent foraging at each canister, and on number of visits to canisters, with food presence/absence as the main effect and trial as a fixed effect. We found a significant effect of food presence on the time adults spent foraging at each canister, and on number of visits to each canister, both for the full 10-minute trials and during the first

3 minutes (Table 3.3). We also found a significant effect of food presence on the time juveniles spent foraging at each canister for the first 3 minutes of trials, but the effect was not significant for the full 10 minutes (Table 3.3). The effect of food presence was not statistically significant for number of visits to each canister by juveniles, either for 10 minutes or 3 minutes. Therefore, the presence of a food reward was not an important factor for juveniles deciding where to forage over the entire 10 minutes of the trials. Based on these results, we decided to conduct further analyses for both the full 10 minutes and for only the first three minutes of trials.

	Adults		Juveniles	
	Time foraging (s)	Number of visits	Time foraging (s)	Number of visits
10 minutes	$F_{1,18}$=3.5; p=0.0747 baited > un-baited	$F_{1,18}$=6.5; p<0.0195 **baited > un-baited**	$F_{1,9}$=0.46; p=0.5138 baited>un-baited	$F_{1,9}$=0.00; p=0.935 un-baited>baited
First 3 minutes	$F_{1,18}$=11.42; p<0.0033 **baited>un-baited**	$F_{1,18}$=12.70; p<0.0022 **baited>un-baited**	$F_{1,9}$=10.40; p<0.0104 **baited > un-baited**	$F_{1,9}$=2.97; p=0.1190 baited>un-baited

Table 3.3 Effect of the presence of a food reward (baited condition) on foraging behavior. For adults, time foraging and number of visits to the food-containing canister were significantly greater than at canisters not containing food. For juveniles, this effect was only significant for time foraging during the first 3 minutes of trials. Statistically significant differences are in bold.

Food-offering Calls as an Attractant

Contrary to predictions, tamarins did not forage at C3 when C3 had the food reward more than at C2 when C2 has the food reward when baited trials were compared. Across the entire experiment, mean time spent foraging was greater at C2 relative to C3, both during the first 3 minutes and for entire 10 minutes of trials, and for both adults and juveniles (Table 3.4).

	Adults		Juveniles	
	Canister 2	Canister 3	Canister 2	Canister 3
10 minutes	67.33±16.92	43.87±13.95	170.5±48.14	132.9±48.14
First 3 minutes	26.33±6.39	11.67±3.26	50.75±15.86	30±12.00

Table 3.4 Mean time spent foraging (s) at canister 3 for trials where C3 contained food versus at canister 2 for trials where C2 contained food during condition one. Adults and juveniles foraged at food-containing C2 more than at the food-containing C3 during condition one.

Canister Design and Canister Position

Because the positions of the canisters changed for each trial, we categorized the canisters into the following three categories and compared foraging efforts at each:

1. 'Predicted if attending to position' or 'PP': Canister predicted to be preferred if tamarins associated the food reward and/or food call with a given foraging position in the enclosure.
2. 'Predicted if attending to design' or 'PD': Canister of a given design predicted to be preferred if tamarins associated the food reward and/or food call with canister design.

3. ‘Predicted to be un-preferred’ or ‘PU’: Canister predicted to be un-preferred since this canister neither contained the food reward in the previous trial nor was at the position that contained the food reward in the previous trial.

For example, for trial 2, C2 (at position 1) was ‘predicted if position’, since in the previous trial, position 1 had the food reward (see Table 3.2 for a summary of canister arrangement for each trial); C3 was ‘predicted if design’, because C3 had the food reward in the previous trial (in this case, at position 1); C1 at position 2 was ‘predicted to be un-preferred’ because C1 was the control canister (it never contained a food reward) and position 2 did not contain the food reward in the previous trial. To look at the effect of canister category we only considered foraging behavior for the un-baited trials so that a food-reward and the call recording were not immediately influencing tamarin foraging decisions. Analyses were performed separately for adults and juveniles.

We examined whether tamarins preferentially foraged at the canister or the position that contained the food reward in the previous trial using a linear mixed model analysis of variance incorporating repeated measures for time spent foraging and for number of visits at each category of canister (PP, PD, PU), with canister category as the main effect and trial as a fixed effect. Adults visited canisters PP significantly more than other canisters during the full 10 minutes ($F_{2,36}$=4.02; p<0.0266; Table 3.5). Adults tended to spend more time foraging at PP than at PD and PU, but this effect was not statistically significant either for 10 minutes or for the first 3 minutes. Juveniles spent significantly more time foraging at PU than at PP or PD during the first 3 minutes of trials ($F_{2,18}$=5.87; p<0.0109); this effect approached significance for the full 10 minutes

of trials ($F_{2,18}$=3.44; p=0.0545; Table 3.6). The effect was not significant for number of visits to each canister category, although visits to PU were on average higher than for other categories during 10 minutes and 3 minutes of trials. Thus, adults in our study concentrated their foraging efforts on canisters 'predicted if attending to position' (PP), but juveniles actually concentrated foraging efforts at canisters 'predicted to be un-preferred' (PU).

Adults (n=4)						
	Time foraging (s)			Number of visits*		
	PP	PD	PU	PP	PD	PU
10 minutes	61.04± 13.19	37.63± 7.86	47.26± 10.60	5.0± 0.91	4.44± 0.74	3.56± 0.63
First 3 minutes	19.11± 4.42	13.63± 3.17	17.37± 4.23	1.56±0.27	1.96±0.36	1.33±0.30

Table 3.5 Mean adult time foraging (s) and number of visits to each canister category (PP, PD, PU) for trials of condition two. *For effect of canister type on number of visits during first 3 minutes of trials, generalized linear mixed model did not converge; effect not significant using a linear mixed model.

Juveniles (n=3)						
	Time foraging (s)			Number of visits*		
	PP	PD	PU	PP	PD	PU
10 minutes	47.72±16.18	71.67±25.56	131.50±28.55	3.89±1.11	5.44±1.48	8.22±1.77
First 3 minutes	18.33±7.56	16.94±6.70	52.89±12.21	1.33±0.40	1.61±0.46	2.67±0.55

Table 3.6 Mean juvenile time foraging (s) and number of visits to each canister category (PP, PD, PU) for trials of condition two. *For effect of canister type on number of visits, generalized linear mixed model did not converge; effect not significant using a linear mixed model.

Changes in Foraging Preferences across Trials

The tamarins in our study did not show significant changes in their preference for foraging at C1, C2, or C3 over the course of the trials; separate linear regression analysis for adults and juveniles was not possible due to small sample sizes. However, trends in foraging activity at each canister across trials suggest that tamarins began to learn which canisters were productive.

We used a linear mixed model analysis of variance incorporating repeated measures to examine how tamarin foraging activity at each canister changed across the un-baited trials. Adults and juveniles were analyzed together. There was no significant effect of canister type on time foraging or number of visits across trials. There was, however, a consistent trend, in that foraging activity at C3 increased slightly across trials (b_1= 2.9717, $t(4) = 1.49$, $p = 0.210$; $F_{1,4}$=2.23, $p = 0.166$), and activity at C1 decreased slightly (b_1= - 4.16, $t(4) = -1.69$, $p = 0.167$; $F_{1,4}$=2.87, $p = 0.166$). Foraging at C2 essentially remained the same across trials with a large variance (b_1= -0.57, $t(4) = -0.28$, $p = 0.79$; $F_{1,4}$=0.08, $p = 0.796$). Results were consistent for time foraging and number of visits.

Although sample sizes are small and variation is large, a trend across trials for adult and juvenile foraging trends suggests an increased preference for C3. Juveniles' mean time spent foraging tended to decrease at C1 across trials, while time foraging increased at C3 and at C2 across trials (Figure 3.2). The trend for juveniles to forage more at C3 was more pronounced than at C2, which is the direction predicted in our hypotheses. Adults' time spent foraging tended to decrease at C1 and C2, and increase at

C3. Time foraging at C1 decreased the most across trials for adults, while time foraging at C2 decreased slightly (Figure 3.3).

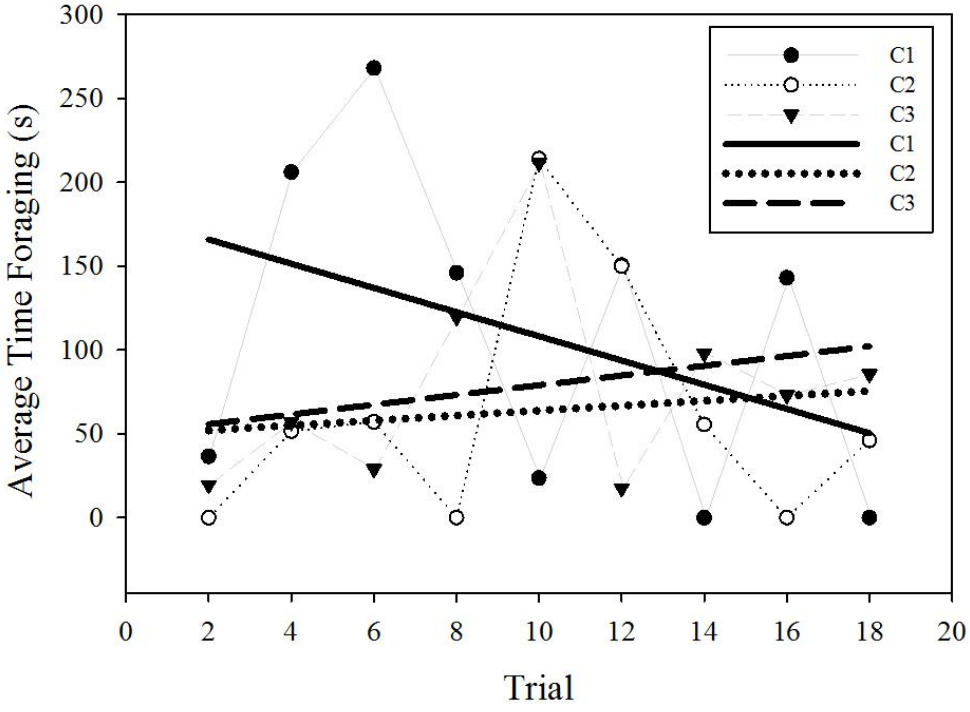

Figure 3.2 Mean time spent foraging by juveniles at the three foraging canister during 10 minute baited trials. Time spent at C1 decreased over the course of the trials (b_1= −7.22), and time spent at C2 and C3 increased, with the largest increase seen at C3 (C2: b_1= 1.47; C3: b_1=2.90).

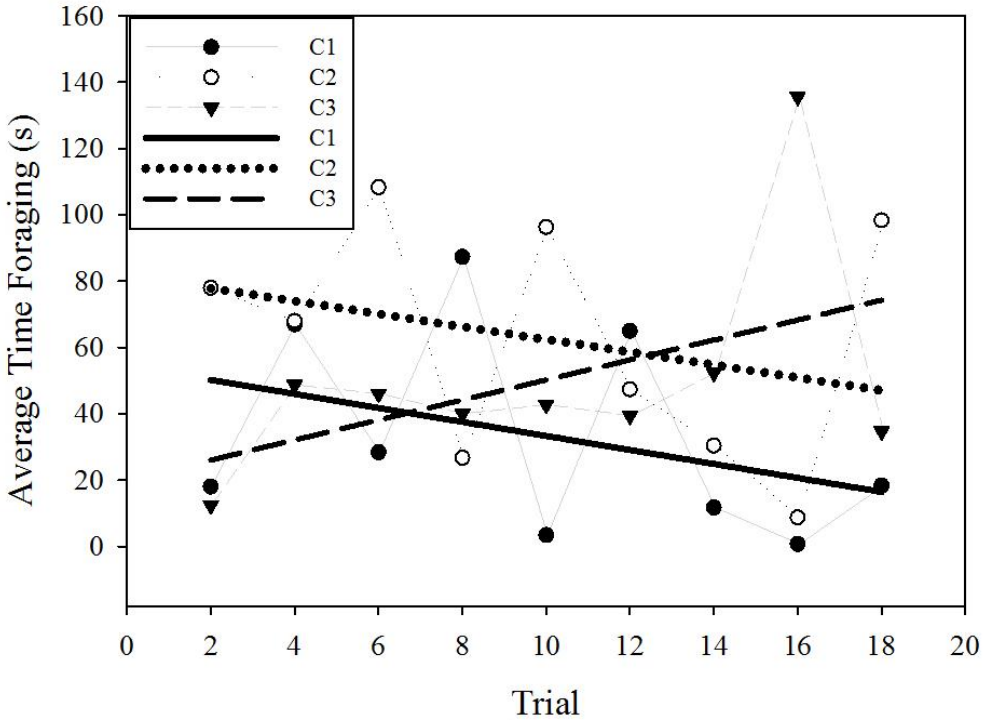

Figure 3.3 Mean time spent foraging by adults at the three foraging canister during 10 minute baited trials. Time spent at C1 decreased over the course of the trials (b_1= −2.22), as did time foraging at C2 (b_1= −1.93). Time foraging at C3 increased across trials (b_1=3.02).

DISCUSSION

Adults and juveniles differed in their response to the foraging canisters in our study, but the food-offering vocalization did not have a strong effect on tamarin foraging activity. While we expected tamarins to forage at C3 more than at C2, especially during condition one trials, this was not the case. Both juveniles and adults, on average, spent more time foraging at C2 than at C3 during the baited trials, indicating that the food-offering call did not influence tamarin foraging decisions, at least not immediately. Since wild tamarin juveniles are immediately attracted to the food-offering call [Rapaport 2011], it is unclear why the juveniles in our study did not show an attraction to the playback call. One possibility is that juveniles were excluded by competition from the adults from food-containing canisters. This possibility is suggested by our results for food motivation, which show that adults spent significantly more time at food-containing canisters and juveniles spent significantly more time at PU. Another possibility is that the quality or noise volume of the playback was startling to the tamarins. Indeed, during some trials in which the playback call was emitted, the tamarins did show a temporary startle response to the noise. Since tamarins food-offering call during the baited trials did not influence the tamarins to prefer to forage at the canister with the call, we suspect that foraging decisions during non-baited trials were influenced primarily by the presence of the food reward rather than by the playback vocalization. Nevertheless, lack of a response to the food-offering call by adults is not surprising given that this vocalization is specifically directed at juveniles in the context of caretaking behavior [Rapaport & Ruiz-Miranda 2002; Rapaport 2011].

Trends in foraging activity across trials suggest that tamarins learned to recognize C2 and C3 as productive foraging sites, and began to avoid C1, which never contained a food reward nor emitted the food call. Interestingly, time spent foraging increased most quickly for C3 for juveniles, which is the trend predicted by our hypothesis; that is, we expected to see foraging at C2 and C3 increase over the course of the experiments, and expected that the effect would be stronger for the canister emitting the food-offering call. In addition, adults increased time foraging at C3 over the course of the un-baited trials, but time foraging at C1 and C2 decreased. Although inconclusive, these results suggest that juveniles did learn to associate both C2 and C3 with food, and that they became increasingly interested in C3 due to the presence of the food-offering call. The increasing trend at C3 for adults may also indicate a response to the food-offering call. Alternatively, the increasing trend for foraging at C3 could simply reflect increasing familiarity with the playback vocalization such that tamarins were less startled by the noise. These trends also indicate that adults and juveniles increasingly avoided C1, which never contained a food reward. If these trends reflect real changes in foraging activity in reaction to canister design, then our study also supports other evidence that callitrichids can retain information on the meaning of abstract symbols (Tanaka et al. 2011). In Tanaka et al. [2011], marmosets (*Callithrix jacchus*) maintained a memory for the meaning of abstract symbols (analogous to our canister designs) for up to three years. Similarly, our tamarin subjects may have been learning which canisters were productive based on canister design.

Adults were motivated by the presence of a food reward in their foraging decisions during the entire 10 minutes of the baited trials. The presence of a food reward only appeared to influence juvenile foraging activity for the first 3 minutes of trials. We suspect that the presence of a food reward was not a strong motivator for the entire 10 minutes of the trial for juveniles because the food reward was usually depleted before 10 minutes passed, and perhaps because the tamarins continued to interact with the canisters for lack of other enrichment in the enclosure. Because the juveniles were not motivated to forage at the food-containing canister over the other canisters when considering the full 10 minutes of trials, these may not have been ideal conditions for the tamarins to strongly associate food with a particular position or canister design. Most likely, the juveniles were so enthusiastic about exploring the canisters for lack of other enrichment that they were highly motivated to forage in any of the canisters, whether or not they contained food. This factor may have affected adults as well; the presence of food significantly predicted the number of visits adults made to canisters, but not time foraging for the entire 10 minutes of trials. Furthermore, our decision to conduct trials before scheduled feeding times may have had an undesirable effect. While we hoped that conducting trails before feedings would make the tamarins highly motivated to explore the canisters, they may have been so hungry that they were overly motivated – that is, they were so eager to find food that they could not focus on the task as we had hoped. If this were the case and high motivation levels interfered with tamarins' attention to the task, this may have resulted in a large amount of variation in foraging behavior.

During the un-baited trials, adults collectively focused foraging activity at the canister predicted to be preferred if tamarins associated the food reward with certain foraging positions in the enclosure. This effect was significant for number of visits but not for time spent foraging. Other studies have shown that callitrichids have a detailed spatial memory [Garber 1989; Moscovice & Snowdon 2006; Porter & Garber 2013], which is also supported by our results. Callitrichids maintain a detailed memory of the location of many feeding trees in the wild [Garber 1989; Porter & Garber 2013]. Captive cottontop tamarins (*Saguinus oedipus*), interacting with a foraging device that had discrete food compartments, showed evidence of memory for correct food compartments 17 months after initial interaction with the device (Moscovice & Snowdon 2006). In our study, memory for the location of the canister that had contained food in the previous trial was only tested over a very short duration of time (5-6 hours). Our results also suggest that, to a significant extent, adults used the most recent information in making foraging decisions; i.e., they concentrated their foraging efforts at the position that contained the food reward in the previous trial. Therefore our assumption that tamarins would prioritize the most recent information on food presence in their foraging decisions during design versus position analysis was satisfied.

During the un-baited trials, juveniles spent the greatest amount of time at the canister predicted to be un-preferred relative to the other canisters, and visited PU, on average, more than the other canisters. Significantly greater foraging activity at PU suggests that juveniles did not pay close attention to which canister contained a food reward during condition one. Alternatively, since adults did indicate a preference for PD

and PP, it is possible that adults were monopolizing those canisters, although overt displays of aggression or chasing were very rare.

We believe that tamarin response to the food-offering call is worthy of further exploration, as our study did not reflect the reaction of wild tamarin juveniles to the food-offering call. We suggest that further experiments involving this vocalization playback should incorporate a period of habituating tamarins to the playback call, and should decrease the volume of the playback if tamarins exhibit a startled response when the recording is played. Given the possibility that juveniles were excluded from food-containing canister by adults, future studies should consider conducting experiments for adults and juveniles separately. Conducting experiments with juvenile-adult pairs, as in Humle & Snowdon [2008] could be another possibility, so that juveniles are not stressed by being isolated from their group. Adults in the juvenile-adult pairs did not exclude juveniles from the foraging apparatus in that study [Humle & Snowdon 2008]. We also suggest that future experimentation be conducted under different environmental conditions in order to reduce what we believe were the effects of an under-stimulating environment and limited space in the enclosure. Specifically, the experiments would ideally be conducted with callitrichids that are free-roaming in captivity (as opposed to animals housed indoors). Free-roaming animals are surrounded by more sources of enrichment and are not as confined as the study subjects in our experiment. Because the animals would be less confined, approaches and attraction to a canister should be more obvious than in an enclosed environment where movement is very limited. Next, we suggest that experiments take place after normal feeding times, so that the subjects are

not overly excited to find food and therefore might be more discriminating in their foraging decisions. Finally, the experiments would benefit from a larger sample size of tamarin participants.

The experiments we conducted allowed us to control for the position of foraging sites across trials by changing the positions of canisters changed between trials. This allowed us to test whether the tamarins developed a preference for certain canister designs without confusing the effect of a preexisting bias for foraging at certain locations, and reduced the effect of training the tamarins to associate food with any one foraging site. As a result, our experiments tested the hypothesis that tamarins learn to recognize productive foraging substrate types more robustly than the hypothesis that they learn specific foraging locations that are productive. Specifically, we were able to look at foraging preference for each canister over the course of the trials. However, we could only test whether tamarins were learning specific foraging locations associated with the call by making the assumption that they were only using information from the previous trial. Playback experiments using a set of identical foraging substrates, where the playback call was emitted from only one location, would be beneficial for determining whether tamarins learn specific foraging locations via interactions associated with the food-offering call.

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CHAPTER FOUR

CONCLUSIONS

The overall objective of this study was to examine co-foraging during juvenile lion tamarin development and to test tamarin foraging response to the food-offering call. Detailed reports of lion tamarin co-foraging have not previously been published. Neither has lion tamarin response to the food-offering call been empirically tested and reported prior to this study.

The second chapter reports our study of co-foraging behavior in wild golden lion tamarins. We found that co-foraging and related behaviors develop slowly in lion tamarins relative to a similar callitrichid species, the common marmoset. This finding supports the contention that lion tamarin specialization in extractive foraging necessitates a longer period of juvenile dependence on adult conspecifics. At 10-14 months of age, juveniles were still engaging in co-foraging and related behaviors at higher rates than adults. Our study also supports the information hypothesis, and therefore provides evidence that co-foraging is important for providing information about food- or foraging-related activities to young lion tamarins. To know exactly what type of knowledge young lion tamarins are gaining via co-foraging would require rigorous experimentation and is beyond the scope of this study. Based on our finding that interest in co-foraging for hidden prey was greater than for surface prey, this study recommends future exploration of the possibility that co-foraging is an important factor in helping juveniles learn to identify productive prey foraging microsites.

Chapter Three examines tamarin response to the food-offering call, a specific vocalization used to initiate the transfer of food to juveniles and to initiate adult-directed foraging. Limited sample size and high motivation to forage affected our ability to determine significance of some findings in Chapter Three. Therefore we recommend further experimentation, ideally involving captive free-roaming tamarins in order to minimize what we believe was the effect of an under-stimulating environment that produced very high motivation to forage. Based on our results showing that juveniles may have been excluded from productive foraging sites by adults, future experimentation should also consider conducting separate experiments with adults and with juveniles. Conclusive evidence that lion tamarins do learn to recognize productive foraging sites more quickly when they are associated with the food-offering call would provide evidence that adult-directed foraging satisfies Caro & Hauser's fourth and final criterion for teaching. Future experimentation aimed at determining exactly what information tamarins perceive from the food-offering call would add to our understanding of the role of this vocalization in the development of foraging skills.